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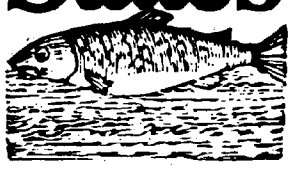

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published by
The Conservation Foundation
Washington, D.C.
in cooperation with
National Oceanic and Atmospheric Administration
Office of Coastal Environment

GB459.4 .038 1974
959659

FEB 5 1997

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$28.00 (if payment accompanies order)
$30.00 (if billing is required)

Published: June, 1974

Preface

Coastal Ecological Systems of the United States was originally prepared for the Federal Water Pollution Control Administration as part of the National Estuarine Pollution Survey conducted in 1968 and 1969. It was the product of a group of scientists led by staff members of the University of North Carolina's Institute of Marine Sciences. Its four volumes include a comprehensive survey of scientific information through 1969, as well as a new system for the classification of coastal ecosystems. The manuscript was submitted to the U.S. Environmental Protection Agency (which absorbed the FWPCA in 1970), but was not published.

The Conservation Foundation is now able to publish this work because of an assistance grant (Grant No. 043-158-68) provided by the National Oceanic and Atmospheric Administration's Office of Coastal Environment, which is responsible for implementing the Coastal Zone Management Act of 1972. The purpose of the grant was to assist the Conservation Foundation in preparing an amended version of this comprehensive work for NOAA's program use. Upon completion of that activity, the Conservation Foundation agreed to make this material available to a wider audience by reproducing the amended manuscript in the most inexpensive way possible.

Those whose personal efforts merit recognition are Robert W. Knecht, director, and Edward T. LaRoe, coastal ecologist, of the Office of Coastal Environment, who foresaw the relevance of this work to the practical needs of coastal zone management; Eugene T. Jensen and A. L. Wastler, of the U.S. Environmental Protection Agency, who arranged for the original study; and John Clark and Laura O'Sullivan of the Conservation Foundation, who, respectively, persuaded their organization to publish this massive work and attended to the myriad details of bringing it into print.

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TIDEPOOLS

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INTRODUCTION

Along rocky ragged shores, spray and waters of high tide may collect forming more or less permanent pools in hollowed-out rock surfaces, in rock crevices or in low areas. Within these tidepools, organisms that are able to adapt to the characteristic environmental conditions found within these systems form communities.

In a study of tidepools in sandstone ledges on the west coast of Vancouver Island, British Columbia, Henkel (1906) found the following life forms in a pool having the dimensions of 3 x 2 x 2½ feet: mussels, gooseneck barnacles, acorn barnacles, chitons, limpets, sea robins, sea urchins, sea anemones, snails, hermit crabs and six varieties of encrusting coralline algae. The chitons and sea robins showed protective coloration, having assumed the color of the rock-encrusting algae which ranged from dark red to light pink and green.

Some of the environmental factors that influence the size and type of tidepool communities that develop are water temperature and salinity, substratum, geographic location, elevation on shore, tidal fluctuation and degree of submergence and exposure, and pool size and depth.

Tidepools are valuable aesthetically as microcosms for teaching and research, as indicators of the quality of coastal waters, as part of the coastal erosive and mineralization cycles, and as an aspect of the recreational value of undisturbed rocky shores.

EXAMPLES

Maine

Johnson and Skutch (1928b) observed nineteen tidepools located on the coast of Mt. Desert Island, Maine. They discussed factors determining distribution of algae in tidepools and concluded that time of submergence and exposure relative to tidal fluctuation determined vertical distribution. Table 1 shows distribution of each algal species in tidepools of sublittoral, lower littoral, and upper littoral zones.

Table 1. Algae distribution in Maine tidepools (Johnson and Skutch, 1928b)

Algae of the Submersible Zone

S. denotes occurrence (outside tide-pools) in the sublittoral belt (−6 to +2 ft.); L., in the lower littoral (2 to 7 ft.) and U., in the upper littoral (7 to 14 ft.); T. denotes the occurrence of the alga in tide-pools of any belt. Brackets indicate that the occurrence of an alga in the habitat designated is exceptional or rare

Species	*Distribution*
Agarum Turneri Post. & Rupr.	S. T.
Alaria esculenta Grew	S. L. T.
Ascophyllum nodosum Le Jolis	(S.) L. U. (T.)
Bangia fusco purpurea (Dillw.) Lyngb.	L. U.
Calothrix crustacea (Schousb.) Born. & Thur.	U.
Calothrix scopulorum (Web. & Mohr.) Ag.	U.
Ceramium botryocarpum Griff. (?)	T.
Chaetomorpha melagonium (Web. & Mohr.) Kütz	T.
Chaetomorpha Sp.? (Rare)	T.
Chondrus crispus (L.) Stack	S. L. U. T.
Chordaria flagelliformis Ag.	S. L. T.
Cladophora constricta Collins	T.
Codiolum longipes Fosl.	L. U.
Corallina officinalis L.	S. T.
Ectocarpus littoralis Lyngb. (= Pylaiella littoralis Kjellman)	L. T.
Elachistea fucicola (Velley) Fr.	S. L. (U.) (T.?)
Elachistea lubrica Rupr.	T.
Enteromorpha compressa (L.) Greville	L. U.
Enteromorpha intestinalis (L.) Greville	T.
Enteromorpha micrococca Kützing	U. (Supra-littoral)
Enteromorpha minima Nägeli in Kützing	L. U. T.
Fucus filiformis S. G. Gmelin	U. T.
Fucus furcatus Ag.	S. L. (U.) T.
Fucus vesiculosus L.	L. U. (T.)
Gigartina mammillosa (Good & Woodw.) J. Ag.	L. T.
Halosaccion ramentaceum (L.) J. Ag.	S. L. T.
Hormiscia penicilliformis (Roth.) Fries	U. (Supra-littoral)
Hormiscia Wormskjoldii (Mert.) Fries	L.
Laminaria digitata (Tum.) Lamx.	S. T.
Leathesia difformis (L.) Aresch.	T.
Melobesia Lenormandi Aresch	S. T.
Monostroma Grevillei (Thuret) Wittrock	L. U.
Petalonia fascia (O. F Müll.) Kuntze	S. L. T.
Petrocelis cruenta Ag.	T. (U.)
Polysiphonia fastigiata Grev.	L. U. (T.)
Polysiphonia violacea Grev.	L.
Porphyra umbilicalis (L.) F. Ag.	L. U. T.
Ralfsia verrucosa Aresch.	T. (Supra-littoral)
Rhizoclonium tortuosum Kützing	(L.) T.
Rhodymenia palmata (L.) Grev.	S. L. T.
Saccorhiza dermatodea De la Pyl	S. T.
Scytosiphon lomentarius Ag.	L. T.
Spongomorpha arcta (Dillw.) Kützing	L. T.
Spongomorpha hystrix Ströfelt	T.
Spongomorpha spinescens Kützing	S. L. (U.) T.
Ulothrix flacca (Dillw.) Thuret in Le Jolis	U.
Ulothrix sp.	T.
Ulva lactuca L.	S. L .T.
Verrucaria striatula (Wahl.) Ach.	U. (Supra-littoral)

New Jersey Marsh Pools

Quite different from rock-bottom tidepools are the pools in the New Jersey marsh described by Moul (1959) some of whose data are given in Table 2. Temperature and salinity ranges are severe in stress for most estuarine organisms, and oxygen deficiencies develop.

California

Bovbjerg and Glynn (1960) studied a small tidepool (one square meter basin) located high in the intertidal zone, Pacific Grove, California. Water was replenished during high tide. A population count showed a large number of individuals (5,185 including 1,670 barnacles, 36 sea urchins, 23 sipunculids and one chiton) but a small number of species (45 species of macroscopic animals and two species of algae), with seven species making up ninety-seven per cent of the animal biomass.

The temperature in the tidepool ranged from 14°C to a maximum of 25°C. Oxygen content ranged from lows of 33% at night to a maximum of 112% during the day. Although Bovbjerg and Glynn found no species that were unique to the tidepool, the pool was a unit, with some cryptic forms, a vertical stratification of barnacles and littorinid snails, and a range of activity and composition varying from day to night.

A similar condition is seen in Batzli's study (1969) where, in the high tidepools, a species of barnacle always ranked second in animal biomass of the system (Table 9). The high tidepool that Bovbjerg and Glynn studied had low species diversity as did the high tidepool described in Batzli's paper.

Bovbjerg and Glynn showed how the study of a tidepool could be a valuable learning experience for students of ecology.

Emery (1946) did a study of the formation and characteristics of high tide rock basins along the California coast near La Jolla. Diurnal variation in water characteristics of one supralittoral pool is illustrated in Figure 1. Emery surmised that the formation of these basins in calcareous rock occurredwhen calcite cement was dissolved from the rock floor. The calcite cement dissolved during the night when the sea water became unsaturated with calcium carbonate as a result of biochemical processes, and tides and snails then removed the loose sand grains. Thus, the basins evolved and eventually coalesced, the broadest and deepest ones being farthest seaward. Similar discussion of tidepool evolution in sandstone rock is found in an earlier study by Henkel (1906) in whichshe recorded observations of pools on the west coast of Vancouver Island. According to Henkel, factors influencing formation of sandstone pools are occurrence of cracks and lines of stratification in the rocks, concretions, carbon dioxide, temperature variations, actions of plants and animals, and erosion by waves, tides and winds.

Emery discussed the importance of high temperature in limiting life in pools, with algae being most abundant in winter when water is coolest and

Table 2. New Jersey tidepools (Moul, 1959)

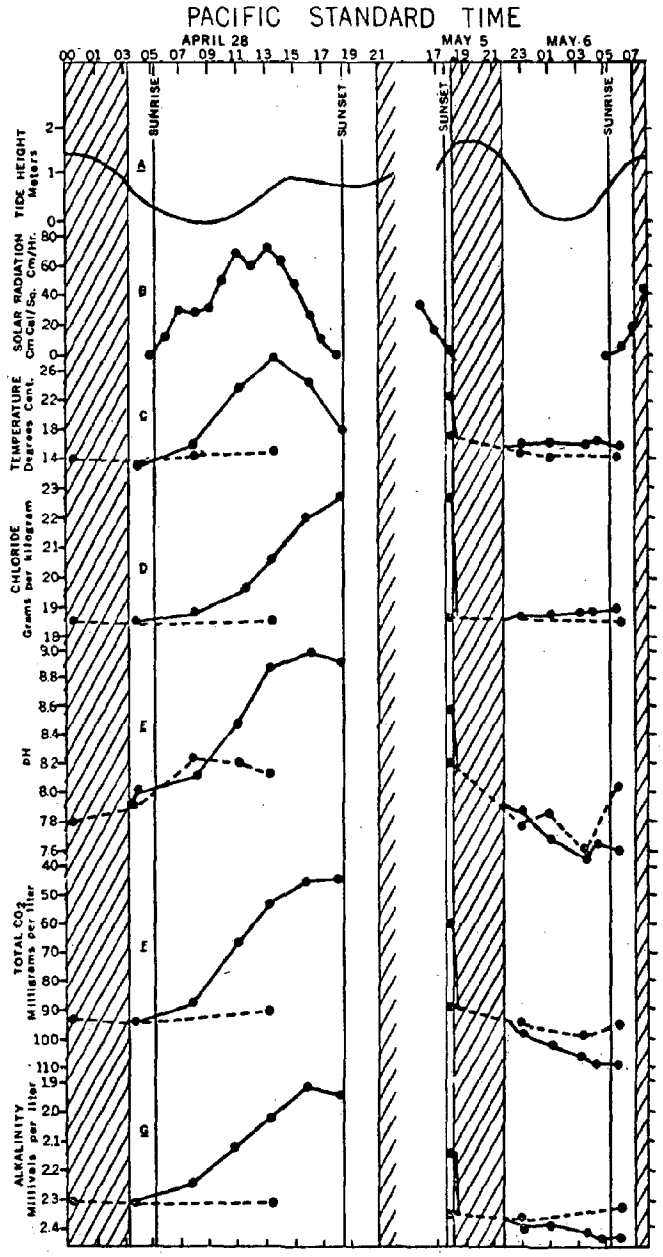
TUCKERTON, NEW JERSEY, 1950

Composite List of Dominant Organisms in Salt Marsh Pools

Organism	6/13	6/21	7/19	8/16	10/6	10/15
Anabaena		X	X			
Calothrix						X
Chroococcus	X		X	X	X	X
Lyngbya	X	X	XX	X	X	X
Merismopedia	X		X			
Oscillatoria	X	X	XX	XX		
Rivularia		X	X	XX		XX
Cladophora	XXX	XXX	XXX	XX	XX	X
Enteromorpha	X	X				X
Rhizoclonium	X	X				
Ulothrix				X		X
Chrysophyte Flag.	X	XX				
Cryptomonads				X	X	
Rhodomonas			XXX		X	X
Amphidinium	XX		X	X	X	XX
Exuviaella		XX	XX	XX	X	XXX
Gonyaulax						XXX
Gymnodinium	XX		XX	XXX	X	
Oxyrrhis			X	XX		
Peridinium	X		X	XXX		XXX
Amphiprora		X	XX	XX		X
Cocconeis	X		X			X
Licmophora	X				XX	XX
Melosira	X					
Navicula	XX		XXX	X	XX	XX
Nitzschia	X	X	XX	XX	XX	XXX

Pool #7 Located about 1/4 mile from marsh edge of Thompson Creek - 1.5 to 2 feet of water in June. Temperatures in degrees Centigrade; salinities in $^{o}/00$.

Date	6/13	6/21	7/19	8/16	10/6	10/15
Temp. (mid-day)	31	--	35	33	17	14
Salinity	31.9	--	49.5	56.7	--	35.7
Surface	open	0.5 open	0.9 open	open	open	open



-Diurnal variation of water characteristics of a supralittoral pool

Dashed line shows variation for ocean water collected near the basin. Cross hatching indicates flooding of basin at high tide. After Emery (1946).

Fig. 1. Diurnal variation of water characteristics of a supralittoral pool on the California coast (Hedgepeth, 1957).

sunlight least strong. By analyzing the size of sand grains excreted by Littorina species, he concluded that these snails are the active erosive agents of sandstone shores. Table 3 summarizes flora and fauna and their degree of abundance in the rock pools.

Washington

Interaction of temperature and salinity is important in determining the population of a tidepool system as well as stratification within that system. Gersbacher and Denison (1930), in their study of four tidepools on the San Juan County coast of the state of Washington, found that larger tidepool animals became more active when the pools were flooded with cool sea water (Table 5). Flooding with freshwater (simulating rain) restricted animal activity as seen in Table 4. When some of the pools were filled with freshwater, the hermit crabs showed much distress and left the pools. Gersbacher and Denison concluded that the kinds of animals and their abundance in tidepools are determined primarily by temperature and composition of the bottom substrtum and that tidepool animals are most active in cold sea water. Table 6 shows temperature and salinity data.

The size of tidepool inhabitants may be related to physical characteristics of the pools. Humphrey and Macy (1930) observed thirty-five rock pools on and in the vicinity of San Juan Island, Washington. In a study of two littorinid snails (Littorina scutulata and L. sitchana), a direct correlation was found between size and temperature. Average volume of the littorinid snails increased with an increase in salinity, temperature, oxygen content, and elevation above high tide, as illustrated in Figure 2.

Batzli (1969) studied community organization in tidepools on the rocky south and west shores of San Juan Island, Washington, by an analysis of biomass (dry weight of organic parts, grams per square meter). He observed six pools, three at low levels and three at high levels, and concluded that the surface-to-volume ratio of a tidepool is the most important factor affecting the physical characteristics of the pool. The following comparisons can be made from Batzli's data, as given in Tables 7 - 9.

Table 3. Algae and animals found in high tide rock basins on the California coast (Emery, 1946).

Algae in the Basins		Animals in the Basins	
Red algae:		**Mollusca:**	
Endocladia muricata	Very abundant in outer basins	*Littorina planaxis*	Very abundant
		L. scutalata	Common
		Tegula funebralis	Common
Polysiphonia simplex	Abundant in August	*Acmaea persona*	Common
		A. cassis pelta	Occasional
Centroceras clavulatum	Occasional	*Callistochiton crassicostatus*	Occasional
Corallina gracilis f. densa	Occasional	*Lepidochitona hartwegii*	Occasional
Gelidium crinale	Occasional	*Mytilus californianus*	Occasional in outer basins
Gigartina canaliculata	Occasional		
Laurencia pacifica	Occasional		
Lithophyllum decipiens	Occasional	**Arthropoda:**	
Petrocelis sp.	Occasional	*Copopoda*	Abundant
Rhodoglossum affine	Occasional	*Balanus glandula*	Common
Brown algae:		*B. tintinnabulum californicus*	Occasional in outer basins
Ralfsia sp.	Abundant		
Ectocarpus granulosus	Abundant in March	*Pachyrapsus crassipes*	Occasional in outer basins
Colpomenia sinuosa	Occasional		
Petrospongium gelatinosa	Occasional		
Green algae:		*Amphipoda*	Occasional
Chaetomorpha californica	Abundant	*Isopoda*	Occasional
Cladophora sp.	Occasional	**Annulata:**	
Enteromorpha sp. (juvenile)	Occasional	Polychaeta worms	Occasional
Ulva californica	Occasional	**Coelenterata:**	
Blue-green algae	Abundant	*Cribrina xanthogrammica*	Occasional in outer basins
Diatoms (sedentary species)	Occasional		
Dinoflagellates	Occasional		

Table 4. Fauna of four tide pools on the coast of Washington state.

Activity before (b) and after (a) adding fresh water.

Pool No.	Number of animals reacting to fresh water						Number of animals in tide pools			
	1		2		3		1	2	3	4
	a	b	a	b	a	b				
Littorina sitchana	0	0	0	0	0	0	500	25	0	400
L. scutulata	0	0	0	0	0	0	1500	100	0	0
Shore crabs	5	0	0	0	0	0	5	0	0	10
Limpets	0	0	0	0	0	0	10	0	50	0
Hermit crabs	225	25	20	20	100	10	300	200	100	0
Mytilus edulis	0	20	0	20	0	0	20	20	0	0
Chrysodomus dira	0	0	0	10	0	0	0	10	0	0
Oligocottis maculosus	0	25	0	10	0	3	35	10	0	0
Chitens	0	0	0	0	0	0	0	5	8	0
Thais	0	0	0	0	0	0	0	8	25	0
Tube worms	0	0	0	0	0	0	0	1	15	0
Calliosoma annulata	0	0	0	0	0	0	0	0	10	0
Decorator crab	0	0	0	0	0	0	0	2	0	0
Isopods	.....		.....		.....		..	2	..	..
Macoma nasuta	.....		.....		.....		..	..	..	51
Cucumaria miniata	0	0	0	0	0	1	0	0	1	0
Small white clams	.....		.....		.....		..	..	..	8
Small Macoma sp	.....		.....		.....		..	..	..	9
Saxidomus giganteus	.....		.....		.....		..	..	..	10
Paphia staminea	.....		.....		.....		..	..	..	56
Balanus cariosus	.....		.....		.....		..	..	..	100
B. glandula	.....		.....		.....		10	25	0	200

Note the decrease in activity of hermit crabs with the addition of fresh water (Gersbacher and Denison, 1930).

Table 5. Activity of Balanus relative to temperature in tidepools on the on the coast of Washington state (Gersbacher and Denison, 1930).

Number of times the cirri of Balanus were extended at various temperatures.

Before flooding Temp. 29° C	After flooding Temp. 17° C	Tide coming in Temp. 26° C	Tide over pool Temp. 14° C
long exposure	long exposure		
26	20	38	80
3	23	0	90
88	10	0	84
7	6	0	70
7	6	39	63
13	6	7	75
12	11	6	95
12	95	6	96
12	30	6	113
14	81	0	86
8	23	0	47
8	14	0	
8	29	14	976
2	66	23	
8	18	0	
8	22	0	
0	2	0	
5	78	5	
3	53	0	
178	637	152	

Note that cirri of the barnacles were extended most frequently at the lowest temperature.

Table 6. Temperature and salinity ranges in tidepools on the coast of Washington (Gersbacher and Denison, 1930).

Range of temperature.

Pool	Level below high tide in cm	Temperature
1	15	13° C–17° C
2	215	14° C–19° C
3	400	13° C–15° C
4	...	14° C–29° C

Results of the titrations for salinity.

Pool	Level below high tide in cm	Normal salinity	After flooding	
			Salinity at surface	Salinity at bottom
1	15	31.13	1.67	28.5
2	215	31.76	.66	6.43
3	400	29.36	19.31	27.59
4	...	31.32	.....	.....
Sea water	...	31.94	....	.....

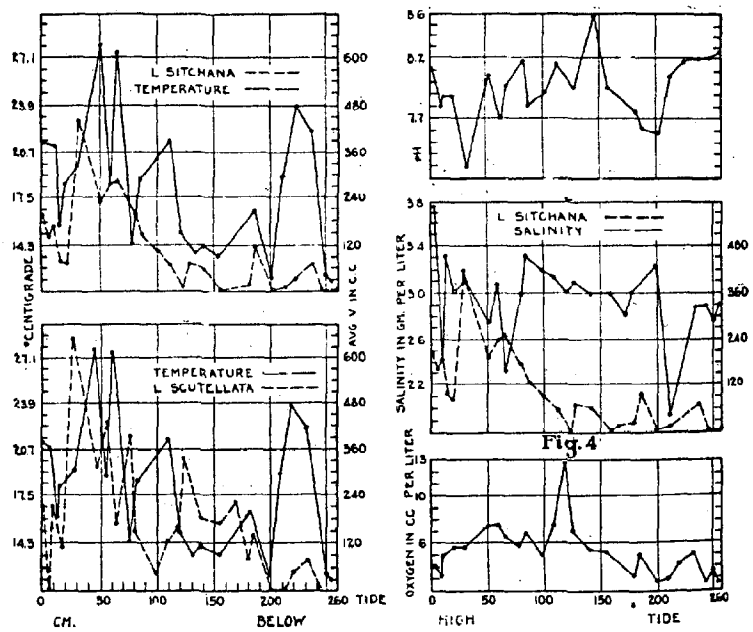


Fig. 4

Fig. 2. The correlation between size of Littorina and temperature, oxygen, salinity and hydrogen ion concentration. The curves represent averages for the various pools when all pools were exposed on clear days, but the same general relation characterized the separate series.

Note the increase in size of Littorina snails with pool temperature. These pools were located on the coast of Washington state (Humphrey and Macy, 1930).

Table 7. Tidepools on the Washington coast (Batzli, 1969).

Comparison of some physical measurements of the tide pools

Pool	Surface area (m^2)	Volume (10^4 cm^3)	Surface/volume
High			
C 3·8	0·141	0·413	0·341
C 3·3	0·225	0·751	0·300
L 3·5	0·699	2·385	0·293
Low			
E 0·8	0·398	1·240	0·321
D 0·5	0·534	3·600	0·148
L 0·5	2·992	28·865	0·104

Table 8. Biomass of flora in tidepools on the Washington coast (Batzli, 1969).

Dry weights of macroscopic flora in the tide pools (g/m^2)

Plant genus	High pools			Low pools		
	C 3·8	C 3·3	L 3·5	E 0·8	D 0·5	L 0·5
Bossiella	–	–	–	–	104·1	312·4
Corallina	41·5	14·2	–	–	149·6	112·4
Phyllospadix	–	–	–	193·7	–	–
Prionitis	–	–	–	0·6	–	8·8
Fucus	18·1	–	–	–	1·3	–
Microcladia	–	–	–	–	3·7	–
Ulva	–	0·9	–	–	2·0	–
Ceramium	–	0·2	–	–	0·5	–
Lethesia	–	–	–	–	0·7	–
Halosaccion	–	–	–	–	0·1	–
Polysiphonia	–	–	–	–	–	<0·1
Lithothamnion (encrusting)	–	–	–	+	+	+
Totals	59·6	15·3	0	194·3	262·0	433·6

Table 9. Animal species in tidepools on the coast of Washington (Batzli, 1969).

Distribution of twenty-seven species which occurred regularly in the tide pools

Taxon	In all pools	In all high pools: But no low pools	In all high pools: And some low pools	In all low pools: But no high pools	In all low pools: And some high pools
Anemones			*Anthopleura elegantissima*		
Polyclads			*Freemania litoricola*		
Polychaetes				*Nereis procera* *Syllis* sp.	*Nereis vexillosa*
Chitons	*Lepidochitona* sp.	*Cyanoplax hartwegii*		*Katherina tunicata* *Tonicella lineata*	
Gastropods	*Acmaea pelta* *A. testudinalis* *Littorina scutulata* *L. sitchana*		*Acmaea digitalis* *Acmaea* sp.	*Searlesia dira*	
Pelecypods					*Mytilus* sp.
Barnacles			*Balanus cariosus* *B. glandula*		
Isopods	*Dynamene sheareri*			*Pseudione giardi*	*Idothea wosnesenskii*
Decapods	*Hemigrapsus nudus* *Pagurus hirsutiusculus*			*Pagurus granosimanus*	
Asteroids				*Leptasterias aequalis*	
Fish				*Oligocottus maculosus*	

Dry weight (g/m²) of organic parts of the five most abundant species in each tide pool

Pool	Rank 1	2	3	4	5
C 3·8	*Anthopleura elegantissima* (135·1)	*Balanus cariosus* (23·8)	*Littorina scutulata* (12·5)	*Acmaea pelta* (9·9)	*Acmaea testudinalis* (8·5)
C 3·3	*A. elegantissima* (348·9)	*B. cariosus* (63·2)	*Hemigrapsus nudus* (36·2)	*Littorina scutulata* (16·9)	*Mytilus californianus* (3·8)
L 3·5	*A. elegantissima* (169·0)	*B. cariosus* (31·6)	*Mytilus californianus* (12·2)	*Hemigrapsus nudus* (1·9)	*Littorina scutulata* (1·8)
E 0·8	*Katherina tunicata* (27·6)	*Searlesia dira* (27·4)	*Pagurus granosimanus* (6·7)	*Acmaea testudinalis* (5·3)	*Hemigrapsus nudus* (3·5)
D 0·5	*K. tunicata* (32·0)	*Thais canaliculata* (16·0)	*Thais lamellosa* (11·9)	*Pagurus hirsutiusculus* (9·6)	*Searlesia dira* (4·2)
L 0·5	*K. tunicata* (28·2)	*Anthopleura elegantissima* (27·4)	*Acmaea testudinalis* (5·9)	*Acmaea pelta* (3·6)	*Pagurus hirsutiusculus* (3·1)

Comparison of the distribution of biomass of animals in the tide pools

Pools	No. of species	Dry weight (g/m²)	No. of dominant species: 75% biomass	No. of dominant species: 95% biomass
High				
C 3·8	22	213·5	2 (9%)	8 (36%)
C 3·3	22	480·0	2 (9%)	4 (18%)
L 3·5	18	223·5	1 (6%)	3 (17%)
Range	18–22	213–480	6–9%	17–36%
Low				
E 0·8	41	87·9	4 (10%)	13 (32%)
D 0·5	35	92·5	5 (14%)	14 (40%)
L 0·5	51	85·3	3 (6%)	16 (31%)
Range	35–51	85–92	6–14%	31–40%

	HIGH POOLS	LOW POOLS
TOTAL SPECIES (range)	18-22	35-51
PLANT BIOMASS (range, g/m^2)	0-60	194-434
DOMINANT PLANT(S)	few species, with corallines dominant	many species, with corallines and surf grass dominant
ANIMAL BIOMASS (range, g/m^2)	213-430	85-92
DOMINANT ANIMAL(S)	sessile filter-feeders (barnacles and sea anemone)	grazer -(chiton)
SURFACE/VOLUME RATIO	largest	smallest (except E 0.8)
DIVERSITY (SPECIES)	least	most

In both the high and low pools a small percentage of the total species present constituted the major part of the biomass, as shown in Table 9.

The high tidepools were dominated by sessile filter-feeders, the barnacle Balanus cariosus and the sea anemone Anthopleura elegantissima. Few plant species were found in the high pools as shown in Table 8. In the low pools, however, there were many plant species present and the animal always ranking number one in biomass in the low pools was a grazing species of chiton, Katherina tunicata.

Hawaii

An illustration of community development in a stable tidepool is discussed by Townsley, Trott and Trott (1962) in their study of a tidepool formed on a lava flow at Kapoho, Hawaii. The tidepool was very large (one acre surface area and 25-foot depth) and was flooded daily at high tide. The water level fluctuated due to water moving through the porous lava. One year after the volcanic eruption a community had developed which included numerous species of herbivores--fishes and gastropods, brackish water shrimp (the dominant crustacean) and algal growth forming mats on the rocks. This tidepool was relatively stable, with a rich population of algae and animals. A second tidepool cut off from the sea was also observed. Table 10 gives a list of the dominant organisms found in each pool.

Canadian West Coast

Klugh (1924) studied six tidepools in ledges of sandstone conglomerate be-

Table 10. Tidepools in Hawaii (Townsley, Trott and Trott, 1962).

Dominant organisms of littoral marine communities in 2 selected areas of the 1960 lava flow at Kapoho, Hawaii, after one year

Area	Dominant organisms
Tide pool	Brown Thallophyta, unidentified Mollusks *Trochus intextus* *Cymatium gemmatum* *Bullaria adamsi* *Dolabella variegata* *Pinna* sp. Crustaceans *Atya* sp. Echinoderms *Echinothrix calamaris* *Actinopyga mauritiana* Fishes *Abudefduf imparipennis* *A. sindonis* *Acanthurus sandvicensis* *Aulostomus chinensis* *Pomacentrus jenkensi* *Fistularia petimba* *Conger marginatus* *Synodus* sp. *Thallasoma duperreyi* *T. umbrostigma*
Opposite tide pool, seaward	Red, brown, green and coralline encrusting algae Mollusks *Cypraea caputserpentis* *Helcionisscus exaratus* *Littorina pintado* *L. scabra* *Melampus castaneus* *Morula* sp. *Nerita picea* *Torinia* sp. *Umbraculum sinicum* *Vexilla striatella* Crustaceans *Grapsus grapsus tenuicrustatus* Echinoderms *Eucidaris metularia* *Tripneustes gratilla*

Table 11. Data from tidepools on the west coast of Canada (Klugh, 1924).

The pools of this series have their connection with the water of the sea severed when the tide reaches the following levels:

Pool	No.	1.	at	a	tidal	level	of	3.5 feet
"	"	2.	"	"	"	"	"	5.8 "
"	"	3.	"	"	"	"	"	7 "
"	"	4.	"	"	"	"	"	12 "
"	"	5.	"	"	"	"	"	14 "
"	"	6.	"	"	"	"	"	19 "

The average time per month during which these tide-pools are uncovered is:

Pool	No.	1.	13½	hours	per	month
"	"	2.	88	"	"	"
"	"	3.	175	"	"	"
"	"	4.	285	"	"	"
"	"	5.	420	"	"	"
"	"	6.	560	"	"	"

Temperature								
of Sea.....		15° C.	14° C.	15° C.	15.5° C.	14° C.	15° C.	Average 14.7° C.
Pool No.	1.	15	14	16	16	14	16	" 15
" "	2.	17	14	19	17	15	17.5	" 16.5
" "	3.	18	15	21	17.2	16	18	" 17.6
" "	4.	22	19	21.5	18.5	22	19.2	" 20.3
" "	5.	26	20.5	26	19.5	24	20.5	" 22.7
" "	6.	28.5	21.5	27	22	25	21.5	" 24.3

tween high and low tide marks at St. Andrews, New Brunswick. Klugh concluded that temperature is the factor limiting plants and animals within these pools. Temperature in pool 6, which is located at the highest level on shore, ranged from 15°C to 28°C in seven and a half hours of exposure on a clear day of sunshine (Table 11). Salinity increased only slightly. The temperature in the three lowest pools, having biota mainly epibenthic (sublittoral) in character, did not rise more than 3°C above the temperature of sea water. No sublittoral species occurred in pools 4, 5, and 6 where the temperature rose more than 3°C above that of sea water. It appeared to Klugh that a rise of more than 3°C is a limiting factor for epibenthic biota. The biota of the pools is summarized as follows:

Pool No. 1. The calcareous red alga, Lithothamnion polymorphum, the Sea-anemone Metridium dianthus, the Holothurians Cucumaria frondosa and Lophothuria fabricii, the Sea-urchin Strongylocentrotus drohbachiensis, the Blood-star Henricia sanguinolenta, the Sun-star Crossaster papposus, the Finger Sponge Chalina oculata, the Tunicate Tethium pyriforme, and the Dog Whelk, Purpura lapillus.

Pool No. 2. Lithothamnion polymorphum, the brown alga Scytosiphon lomentarius with Ectocarpus confervoides growing upon it, the brown alga Desmarestia viridis (present early in the season but disappearing in July), Metridium dianthus, Cucumaria frondosa, Lophothuria fabricii, Strongylocentrotus drohbachiensis and Purpura lapillus.

Pool No. 3. Lithothamnion polymorphum, Scytosiphon lomentarius, the filamentous green alga Hormiscia penicilliformis, the red algae Polysiphonia urceolata and Chondrus crispus, Lophothuria fabricii, S. drohbachiensis, and P. lapillus.

Pool No. 4. Chondrus crispus, Scytosiphon lomentarius, and the bivalves Saxicava rugosa, and Mytilus edulis.

Pool No. 5. Very limited growth of Chondrus crispus, Phyllitis fascia and Scytosiphon lomentarius (both absent in 1921 and present in 1922), and Mytilus edulis.

Pool No. 6. Scytosiphon lomentarius (absent in 1921, limited growth in 1922), Mytilus edulis and Balanus balanoides.

British Isles

In his study of hydrogen ion concentration of sea water of tidepools adjacent to Plymouth Sound, England, Atkins (1922) determined that the rock pool water in the summer was more alkaline (higher pH) than the water of the sound and that the water temperature in these tidepools was, at times, more than 2.5°C warmer than the temperature of water in Plymouth Sound. Atkins attributed the greater range in hydrogen ion concentration to active photosynthesis of algae confined within the rock pools. He also stated that tem-

perature increase would drive off carbon dioxide and thereby decrease hydrogen ion concentration (disregarding other salts and photosynthesis). The alga Fucus evanescens is absent from tidepools due to pH and temperature range, according to Atkins.

Gail (1919) also found at Plymouth Sound that tidepool temperature was too high and pH too extreme to allow Fucus evanescens to grow. Growth of Ulva, a green algal form, also inhibited the growth of F. evanescens because it increased the alkalinity of the surrounding waters. Gail never found F. evanescens in tidepools or in considerable quantity with Ulva. Figures 3 and 4 illustrate the germination of Fucus oospores and the growth of Fucus sporelings as related to pH and temperature. The average temperature (1:00-4:00 p.m.) in the pools studied was 24.7°C. The pH range was 7.43-8.59, and often reached 8.8.

In another related study by Brown (1915), fresh-water was shown to inhibit the growth and reproduction of certain algal species in laboratory experiments.

Littorina zonation in tidepools may be determined by heat coma. Sandison (1967), in studying tidepools on the coast of the British Isles, found that Littorina species succumb to heat coma at a lower temperature in water than in air, as illustrated in Figures 5 and 6 . In air the snails would be more subject to desiccation, as the foot is relaxed when the snail is in heat coma. Heat coma was defined by Sandison as lack of response of a snail to a prick, yet the snails in heat coma attained full recovery of activity if removed to lower temperature. Tidepools would protect Littorina from desiccation if the temperature reached the heat coma range during the day. Sandison observed the behavior of Thais lapillus, Littorina littorea, L. littoralis, L. saxatilis and L. neritoides.

In a study of three tidepools in igneous rock at Scarlett Point, Isle of Man, as shown in Figure 7 , Naylor and Slinn (1958) concluded that the upper pool showed the most variable conditions and the bottom zone of the lower pool was the most stable. Temperature, salinity and oxygen concentration data is given in Table 12. Naylor and Slinn described variation in tidepool flora and fauna according to the level at which the pool was located. Variation in occurrence of isopod species, Jaera nordmanni and J. albifrons and Idotea chelipes, as well as an amphipod species Gammarus duebeni, and a turbellarian Procerodes ulvae, is shown in Table 13. Other species found in the pools were the stickleback Gasterosteus aculeatus, oligochaetes, chironomid larvae, a copepod Eurytemora velox and four types of algae. The limpet Patella vulgata, Littorina snails and the isopod Ligia oceanica were found on and under rocks, in and around the pools.

Some tidepools located on the west coast of Ireland are unusual in that almost all the space in the pools is occupied by the purple sea urchin Paracentrotus lividus. These pools are shallow, slow-draining depressions, as shown (together with shore zonation) by Lewis (1964) in Figure 8 .

Animals migrating into and out of tidepools will affect the pool system.

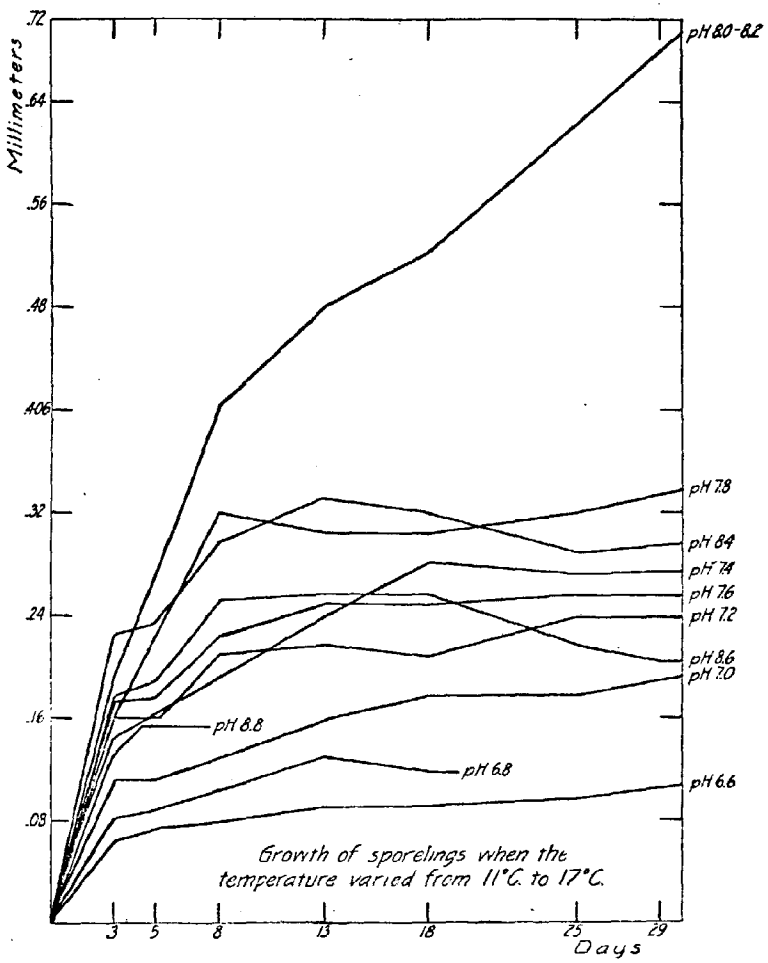


Fig. 3. Growth of Fucus sporlings, related to pH and temperature. pH of these tidepools adjacent to Plymouth Sound, England, often reached 8.8 (Gail, 1919).

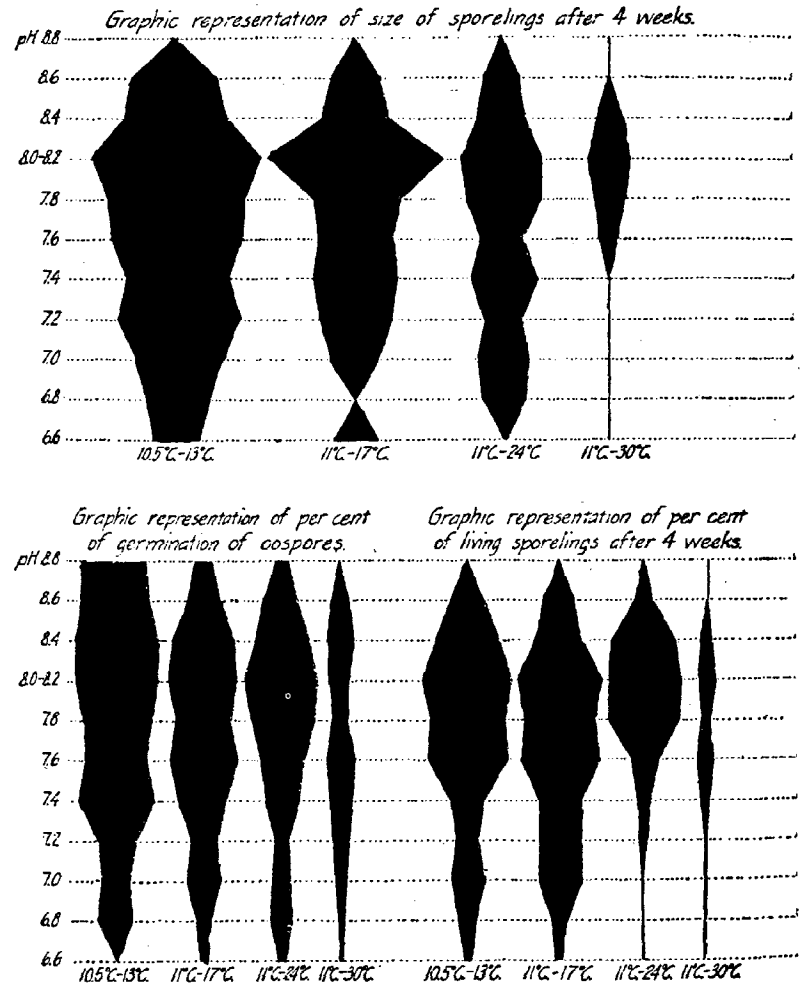
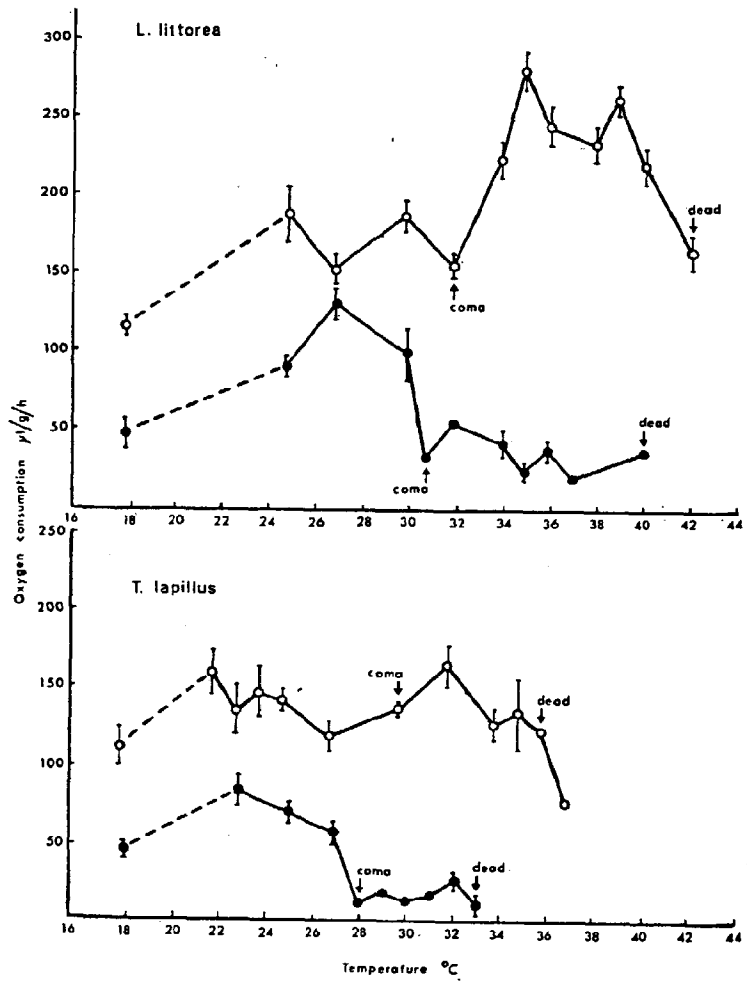
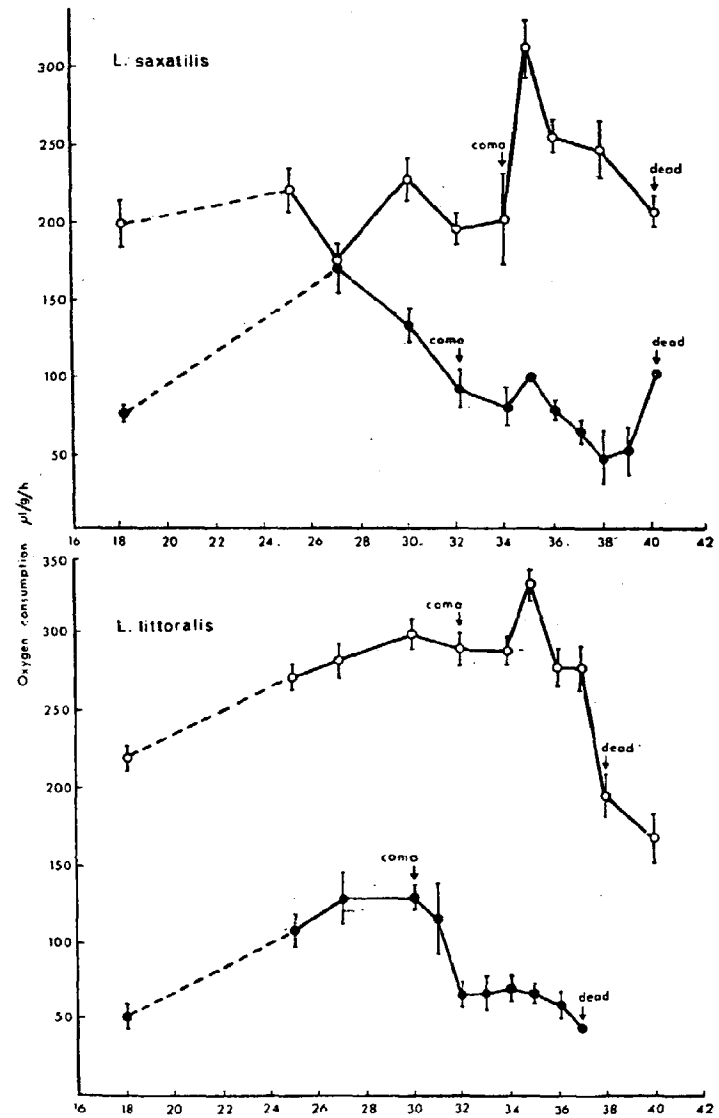


Fig. 4. Germination of oospores and growth of Fucus sporelings. Average tidepool temperature of pools near Plymouth Sound was 24.7° C (1:00-4:00 P.M.) (Gail, 1919).



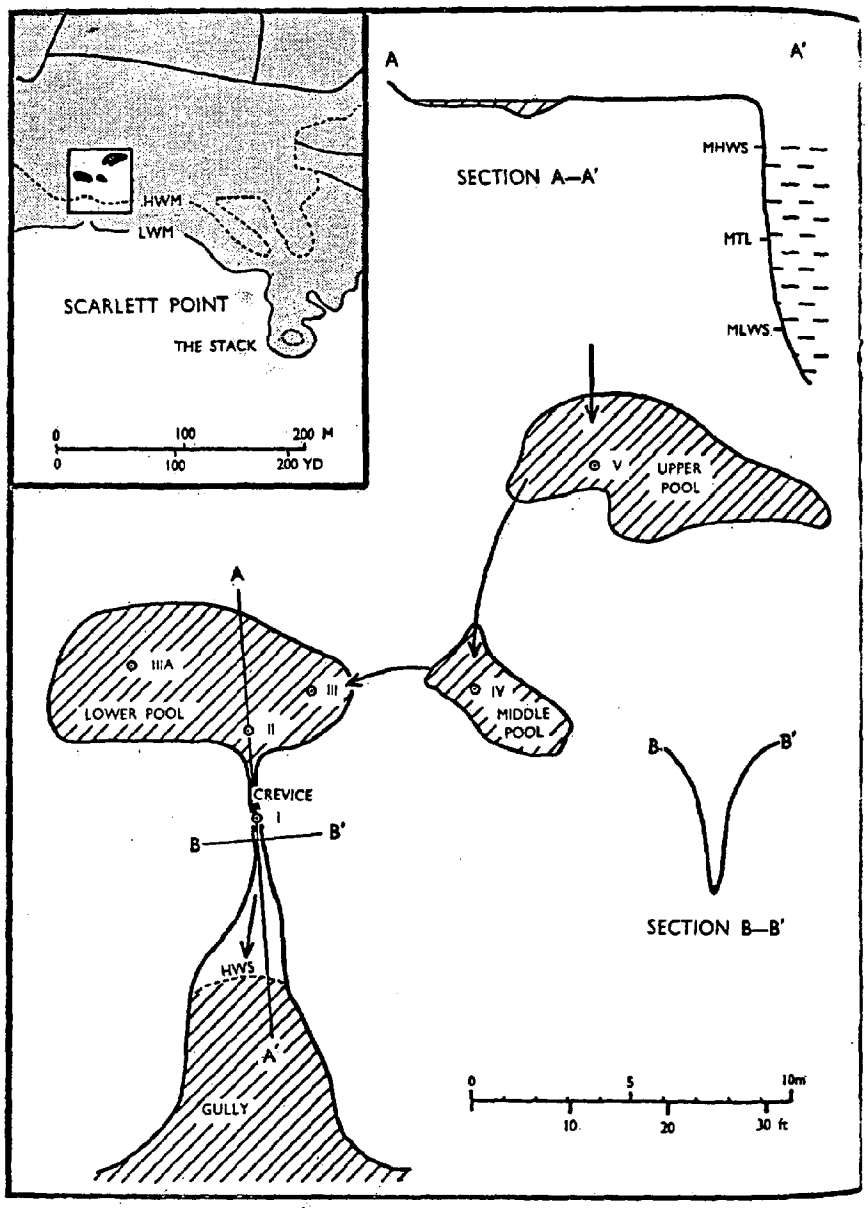
The rate-temperature curves of oxygen consumption of *L. littorea* and *T. lapillus* at temperatures between 18 °C and 42 °C (data at 18 °C are taken from Sandison, 1966). Average rates of oxygen uptake in air (○) and in water (●); limits of twice the standard error are indicated by horizontal bars; where no standard error is shown these limits are so small as to be incorporated in the symbol representing the mean.

Fig. 5. Tidepool littorinid snails in the British Isles (L. littorea and T. lapillus) (Sandison, 1967). Note that heat coma occurred at a lower temperature in water than in air.



The rate-temperature curves of oxygen consumption of *L. littoralis* and *L. saxatilis*. Same conditions.

Fig. 6. Tidepool littorinid snails in the British Isles (L. saxatilis and L. littoralis).



Plan and sections of the pools at Scarlett Point. The horizontal and vertical scales are t same. Arrows indicate the flow of fresh water.

Fig. 7. Tidepools on Scarlett Point, Isle of Man (Naylor and Slinn, 1958).

Table 12. Tidepools on Scarlett Point, Isle of Man (Naylor and Slinn, 1958).

Temperature, salinity and oxygen concentration of the pools at Scarlett Point

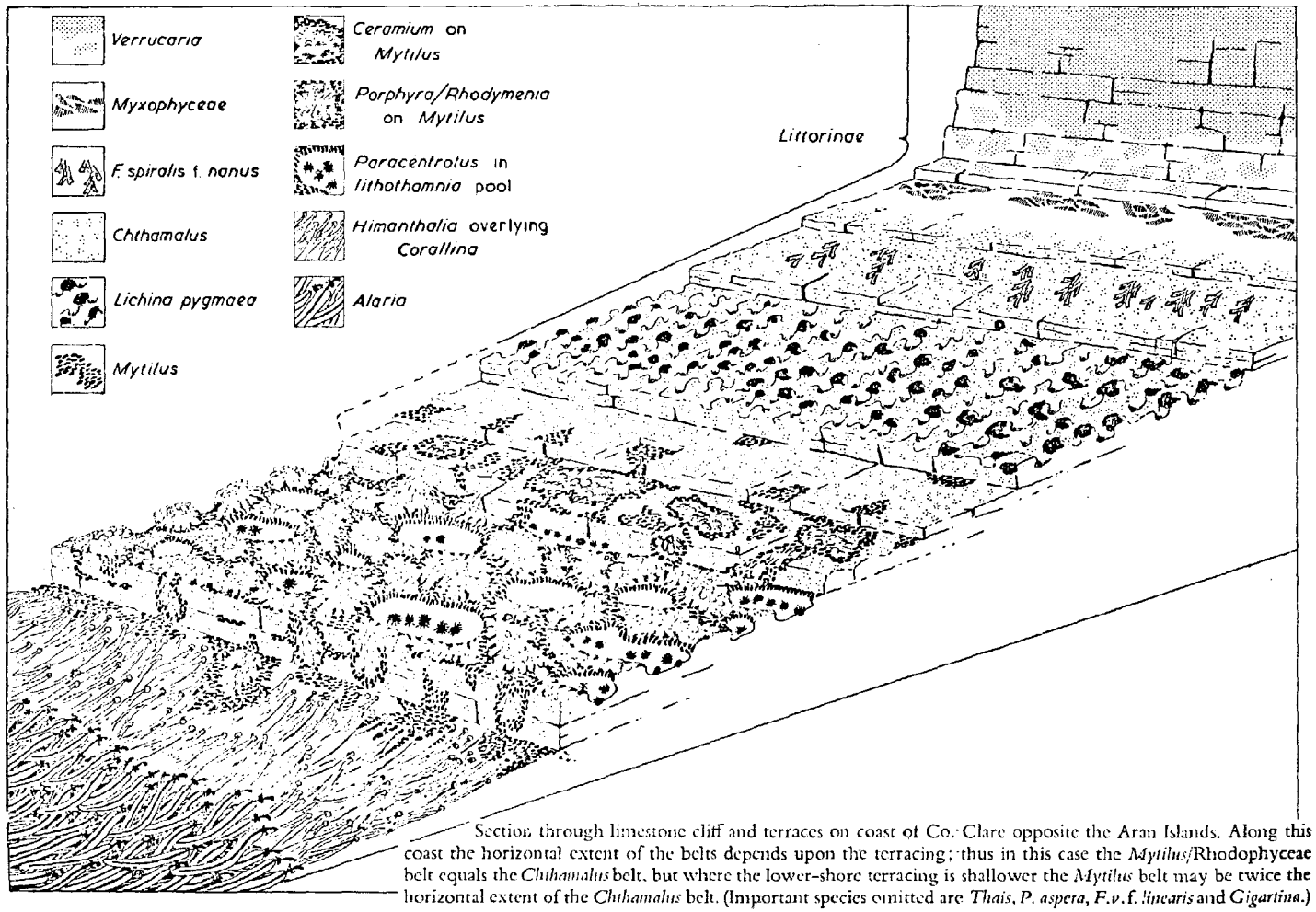
For station positions see Fig 1.

Station	Temperature (°C) surface	Temperature (°C) bottom	Salinity (‰) surface	Salinity (‰) bottom	Oxygen (ml/l.; % sat. in parentheses) surface	Oxygen (ml/l.; % sat. in parentheses) bottom
12 May 1953						
II	9·1	9·1	–	34·3	–	6.55 (100)
III	13·6	13·5	–	34·8	–	4.21 (71)
IV	13·1	12·7	–	19·2	–	5·16 (77)
V	12·4	12·5	–	12·2	–	6·39 (92)
18 January 1954						
II	8·6	8·6	33·3	33·4	7·65 (115)	7·65 (115)
III	–	–	–	–	–	–
IV	8·2	8·2	32·3	32·4	8·38 (123)	8·40 (124)
V	7·4	6·7	21·4	21·5	8·02 (107)	8·38 (112)
30 August 1954						
II	19·2	15·5	33·6	33·8	10·24 (187)	8·54 (148)
III	19·4	17·4	33·7	33·6	9·58 (175)	6·30 (111)
IV	17·6	16·1	33·8	31·7	7·81 (140)	7·58 (130)
V	18·2	16·9	2·2	2·2	8·64 (128)	8·73 (127)
2 November 1954						
II	8·3	11·3	1·6	29·2	8·30 (100)	2·35 (36)
III	8·4	11·1	1·5	29·4	8·28 (100)	2·69 (41)
IV	7·9	11·1	1·2	29·9	8·68 (104)	1·13 (17)
V	8·9	11·1	1·0	20·6	3·57 (44)	3·72 (53)
18 February 1955						
II	1·0	4·0	4·1	29·0	10·60 (108)	10·79 (141)
III	1·0	5·5	2·7	20·2	9·50 (96)	9·09 (117)
IV	2·0	5·0	1·9	22·1	11·42 (118)	10·94 (139)
V	0+	5·5	1·7	29·3	10·25 (101)	20·00 (275)
20 April 1955						
II	19·5	19·5	10·7	25·2	11·19 (181)	8·92 (157)
III	19·8	26·0	10·7	21·2	10·71 (173)	14·72 (280)
IV	17·0	23·0	5·3	11·0	11·24 (167)	14·81 (252)
V	17·0	23·0	5·0	13·3	8·41 (125)	18·30 (314)

Table 13. Occurrence of species in tidepools on Scarlett Point, Isle of Man (Naylor and Slinn, 1958).

Total number of specimens found in a series of six samples in various months over the years 1953-55 at stations I-V (see Fig. 1)

Station No.	*Jaera nordmanni*	*Jaera albifrons*	*Idotea chelipes*	*Gammarus duebeni*	*Procerodes ulvae*
I	4	692	72	61	22
II	86	180	430	121	8
III	264	34	88	108	25
IV	192	–	62	154	51
V	155	–	–	147	22



Section through limestone cliff and terraces on coast of Co. Clare opposite the Aran Islands. Along this coast the horizontal extent of the belts depends upon the terracing; thus in this case the *Mytilus*/Rhodophyceae belt equals the *Chthamalus* belt, but where the lower-shore terracing is shallower the *Mytilus* belt may be twice the horizontal extent of the *Chthamalus* belt. (Important species omitted are *Thais*, *P. aspera*, *F.v.f. linearis* and *Gigartina*.)

Fig. 8. Zonation on west coast of Ireland (Lewis, 1964). Note Paracentrotus lividus in lithothamnia pools. Most of the purple sea urchins have attached algal debris and limpet shells. These pools are shallow, slow-draining. There is little distinction between pool and rock conditions.

The migrants can feed and thereby remove energy from the system, increasing instability (Green, 1968) or add nutrients in the form of waste products. Gibson (1967) studied movement of two species of littoral fishes, Acanthocottus bubalis and Blennius pholis, in and out of seven semi-enclosed tidepools in Wales. The majority of the fish remained in a particular pool less than two weeks. Gibson implied that the fish moved out of the pools to feed. Movement was related to temperature as illustrated in Figure 9.

Australia

Guiler (1960) studied a highly stressed tidepool in Australia characterized by high rainfall and intense wave action. He stated that the dominant species of alga, Phylospora comosa, did not reach maximum development and he attributed this to the stress of wave action.

Japan

Algae are important commercially in Japan. Yendo (1914), in a study of Japanese tidepool flora, stated that the unique vegetation of high-tide pools is dependent mainly on salinity variation and, in warmer countries, probably also on temperature fluctuation. Yendo also related water movement to morphology of Laminaria fronds.

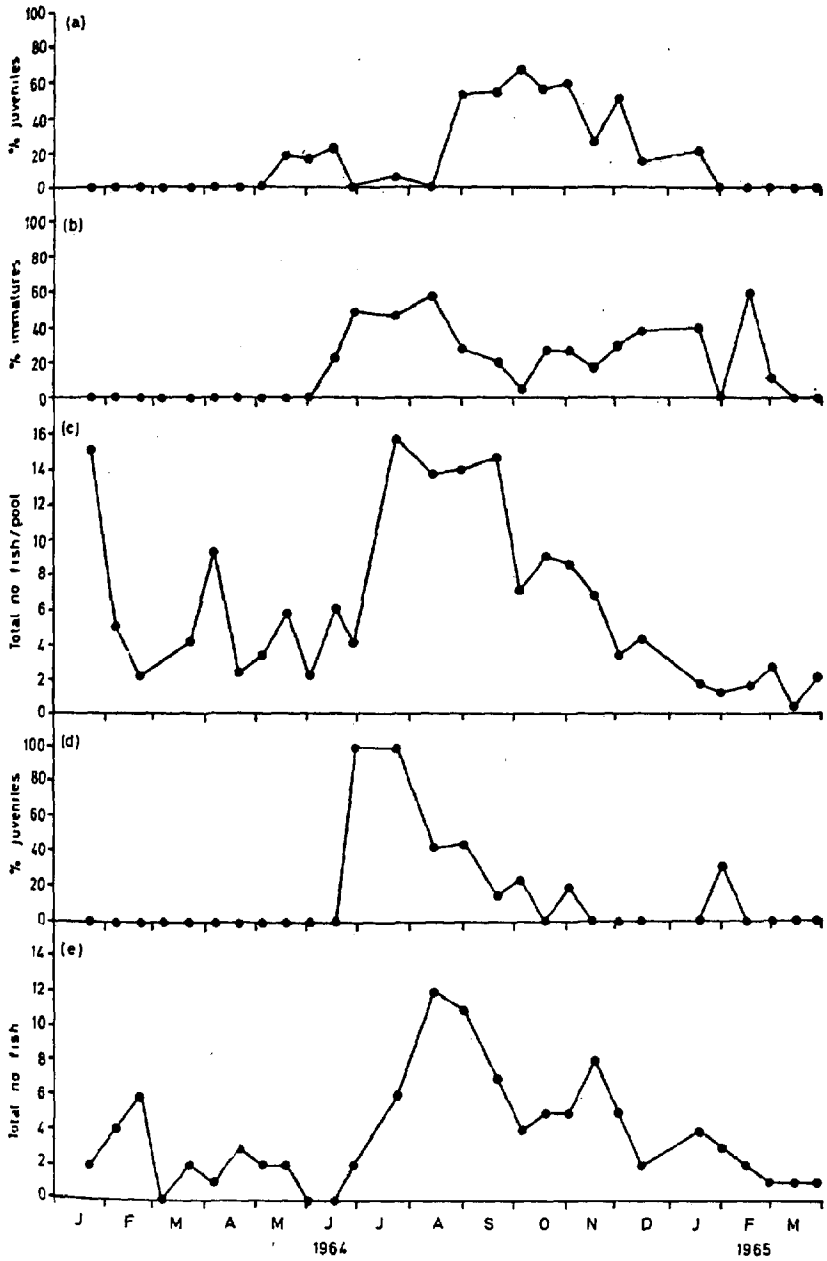
CHARACTERISTICS OF TIDEPOOL ENVIRONMENTS

There are many variables that influence tidepool systems. Some of the conditions which vary in the tidepool environment are discussed in the following paragraphs.

Temperature and Salinity

The water temperatures characteristic of tidepools doubtless serve as a limitation to certain plant and animal species. Water temperature is influenced by geographic location, shading, absorption of heat by the substratum, time and frequency of tidal flooding, freshwater runoff and air temperature. If tidal flooding is early and/or late in the day, the water temperature may tend to follow that of the air, whereas if flooding occurs at midday the tidepool water temperature may suddenly be restored to that of the sea. Lewis (1964) illustrated this phenomenon with graphs of diurnal temperature changes and generalized that water temperature of tidepools tends to follow the temperature of the air rather than that of the sea (See Figure 10). Range in temperature as related to depth is illustrated by Hedgepeth (1957) in Figure 11.

Salinity of tidepool water may vary, especially in more isolated pools; these changes are influenced by evaporation, rainfall and freshwater runoff, and tidal flooding. Significant changes in salinity may eliminate euryhaline species from tidepool habitats. Stratification may occur if freshwater remains as a surface film (Table 14). Violent changes in temperature and salinity may occur with alternating rain and tides, as seen in Table 14 and Figure 12 (Lewis, 1964). Change in animal population with change in pool salinities was charted by Johnsen (1946) and is shown in Table 15.



Variation in the mean number of fish per pool at Porth Cwyfan. (a) % juvenile *Blennius pholis*; (b) % immature *B. pholis*; (c) mean number of *B. pholis* per pool, all age groups; (d) number of juvenile *Acanthocottus bubalis* in Pool B, as % total *A. bubalis*; (e) number of *A. bubalis* in Pool B, all age groups.

Fig. 9. Movement of fishes into and out of tidepools located in Wales. Note the relationship of migration and temperature (Gibson, 1967).

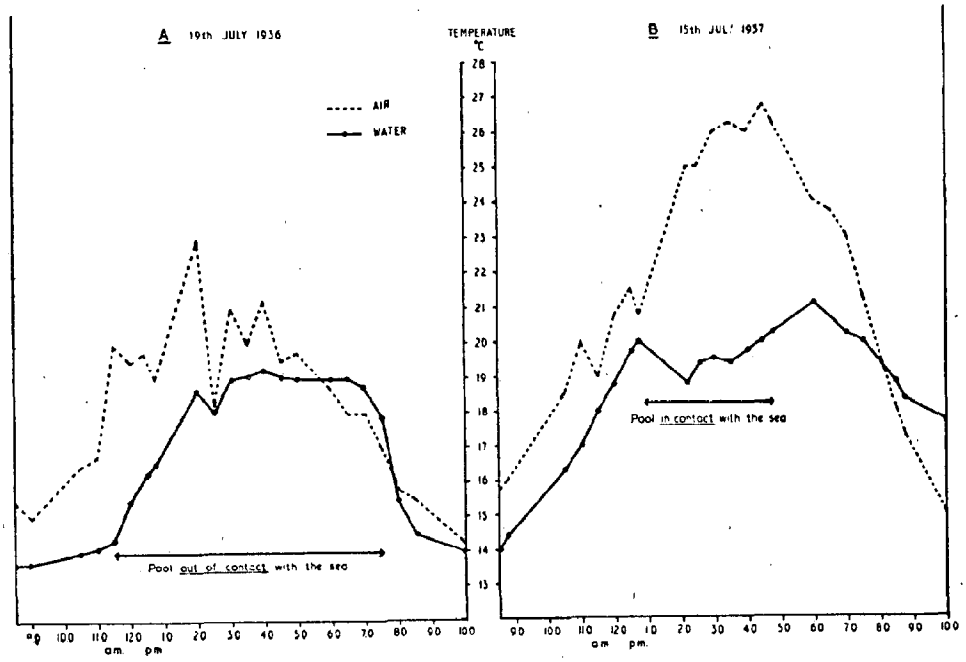


Fig. 10 . Diurnal temperature changes in a pool lying above M.T.L. when A, low water occurs in the afternoon and B, high water occurs in the afternoon. (Re-drawn from Pyefinch [102].)

Water temperature follows air temperature when low water occurs in the afternoon. It is similar to sea temperature when high water occurs in the afternoon (Lewis, 1964).

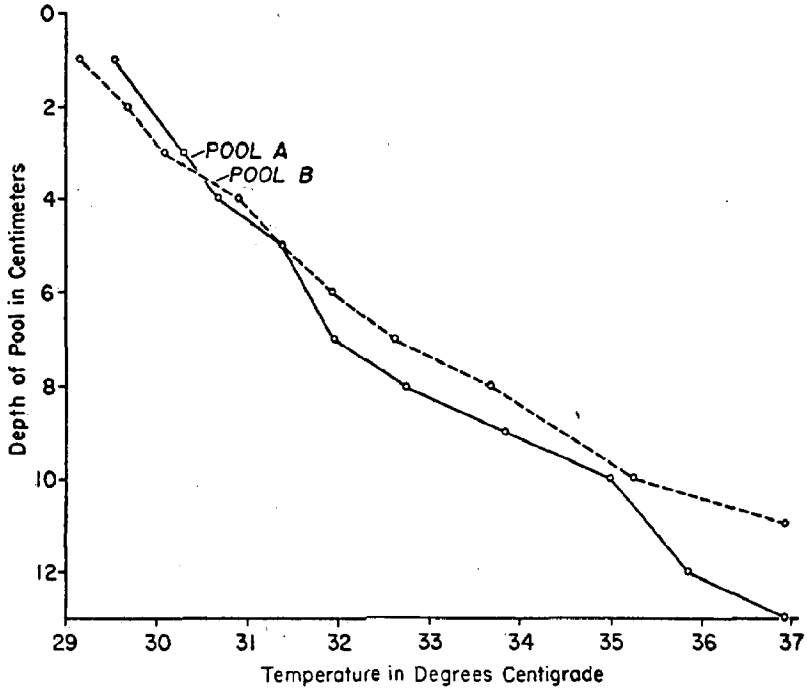


Fig. 11. Temperature stratification with depth in two tidepools (Hedgepeth, 1957, from notes of T. S. Austin).

Table 14. TEMPERATURE AND SALINITY IN TWO HIGH-LEVEL POOLS

Date	Pool	Temperature (° C) Surface	Temperature (° C) Bottom	Salinity (‰) Surface	Salinity (‰) Bottom
12.5.53	I	12.4	12.5	—	12.2
	II	9·1	9·1	—	34·3
18.1.54	I	7·4	6·7	21·4	21·5
	II	8·6	8·6	33·3	33·4
30.8.54	I	18·2	16·9	2·2	2·2
	II	19·2	15·5	33·6	33·8
2.11.54	I	8·9	11·1	1·0	20·6
	II	8·3	11·3	1·6	29·2
18.2.55	I	0·0	5·5	1·7	29·3
	II	1·0	4·0	4·1	29·0
20.4.55	I	17·0	23·0	5·0	13·3
	II	19·5	19·5	10·7	25·2

Pool II lies about 5 ft. above M.H.W.S. but during rough weather is flooded whenever the tide is above H.W.N. level. Pool I is about 3–5 ft. higher. (Data from Naylor and Slinn [95].)

Note salinity stratification in Pools I and II on 12.5.53, 2.11.54, 18.2.55, and 20.4.55. Temperature stratification also occurred on 2.11.54 and 18.2.55, with cooler water at the surface. Cool, less saline water remains as a surface film on the pools (Lewis, 1964).

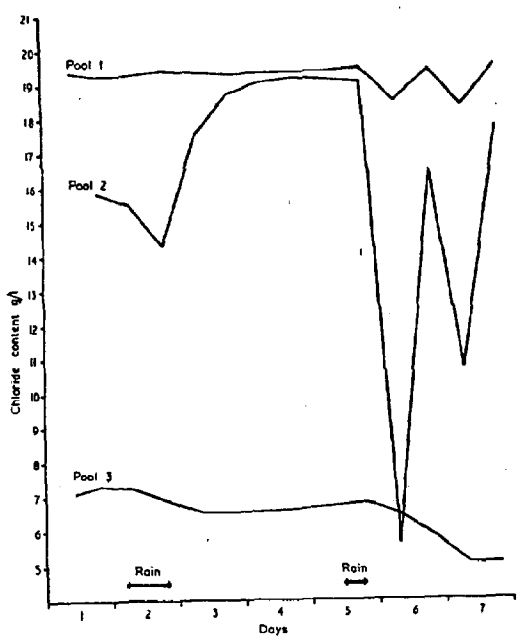


Fig. 12. Salinity changes in pools lying above M.T.L. (Pool 1), above M.H.W.N. (Pool 2) and above M.H.W.S. (Pool 3). Pool 1 was flooded daily by the tide and showed only slight changes while Pool 3 was not flooded by any tide and showed steadily decreasing salinity. Pool 2 was affected by the tide in the middle and later part of the week and the alternating influence of sea and rain caused violent salinity changes. (From Pyefinch [102].)

Note the salinity range relative to the level of location of pool on shore (Lewis, 1964).

Table 15. —*Appearance of the fauna at different salinities*

From Johnsen (1946). (Hedgepeth, 1957).

Animal \ Salinity	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	
Herpobdella lineata	O																																		Only in fresh water
Hæmopis sanguisuga	O																																		
Daphnia longispina	O																																		
Ceriodaphnia megops	O																																		
Anurophorus laricis	O																																		
Libellula depressa	O																																		
Triturus vulgaris	O																																		
Micropterna sequax	O																																		
Piona sp.	O	×																																	
Cyprideptis aculeata	×	×	×																																
Callicorixa limitata	O	(×	×)																																
Coelambus parallelogrammus	×	(×	×)																																
Glyptolendipes sp.	×	×	×																																
Bufo viridis	O	O	O																																
— *calamita*	O	O	O																																
Heterocypris salina	×	×	×	O																															
Candona compressa	×	×	×	O																															
Hydrometra stagnorum	O	O	O	O																															
Callicorixa fabricii	×	×	×	O																															
Anticorixa linnei	×	×	×	×																															
Callicorixa hieroglyphica	×	×	×	O	×																														
Chironomus thummi-Grp.	×	×	×	O	O	×																													
Rana esculenta	O	O	O	O	O	O																													
Dendrocœlum lacteum	×	×	×	×	×	O	×																												
Limnoporus rufoscutellatus	O	O	O	O	O	O	O																												
Callicorixa producta	×	×	×	O	O	O	×																												
Oecetis ochracea	×	×	×	×	×	×	×																												
Limnophilus rhombicus	×	×	×	×	×	×	×																												
Notonecta maculata	O	O	O	O	O	O	O	O																											
Cloëon dipterum	O	×	×	×	×	×	×	×																											
Macropelopia sp.	×	×	×	×	×	×	×	×																											
Limnotrechus gibbifer	×	O	O	O	O	O	O	O	×																										In fresh and brackish water
Notonecta glauca	O	×	×	×	×	×	×	×	×																										
Callicorixa semistriata	×	×	×	×	×	×	×	×	O																										
Ilybius (obscurus)	×	×	×	×	×	×	×	×	×																										
Bufo bufo	O	×	×	×	×	×	×	×	×																										
Aeschna cyanea	O	×	×	×	×	×	×	×	×	×																									
Anophelet maculipennis	×	O	×	×	×	×	×	×	×	×																									
Limnotrechus lacustris	×	×	×	×	×	O	O	O	×	×	×	×																							
Haliplus immaculatus	×	×	×	×	×	×	×	×	×	×	×	×																							
Colymbetes sp.	×	×	×	O	×	×	×	×	×	×	×	×																							
Ischnura elegans	O	O	O	×	×	×	×	×	×	×	×	×	×	×																					
Theodoxus fluviatilis	O	O	O	O	O	O	O	O	×	×	×	×	×	×	×	×																			
Hydrophorus praecox	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	O																		

Animal \ Salinity	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	
Limosina humida	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	O																		
Orthocladiinae sp.	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O																
Nepa cinerea	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×																
Nais elinguis	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×											
Podura (aquatica?)	O	O	O	O	O	O	O	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×											
Bidessus geminus	×	×	×	O	O	O	O	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×										
Hydrobia ventrosa	×	×	×	×	×	×	O	O	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×										
Asellus aquaticus	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×								
Tricholanypus sp.	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×								
Limnotrechus thoracicus	×	O	O	O	O	O	O	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×								
Radix ovata	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O						
Chironomus halophilus-Grp.	O	O	O	O	O	O	O	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×					
Pygosteus pungitius	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×					
Dytiscus marginalis	×	×	×	×	O	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×			
Enchytraeidae	×	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Tubificidae	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Chydorus sphaericus	×	×	×	×	×	×	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Gammarus duebenii	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	
Haliplus lineatocollis	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	In fresh, brackish and salt water
Gyrinus natator	×	×	×	×	×	O	O	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Helophorus guttulus	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	
Enochrus bicolor	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	
Culex pipiens	×	O	O	O	O	O	O	O	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Cricotopus sp.	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Eristalis sp.	×	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Scatella stagnalis	×	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Hydrobia jenkinsi	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	O	O	O	O	O	O	O	O	O	O	O	
Anguilla anguilla	×	×	×	×	×	×	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Gasterosteus aculeatus	O	×	×	×	×	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Pleuronectes flesus	O	O	O	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
*Idothea baltica**		×	×	×	×	×	×	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Sphaeroma rugicauda		×	×	×	×	×	×	×	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	
Ephydra riparia		O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Hydrobia ulvae		×	×	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	
Mytilus edulis		×	×	O	O	O	O	O	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Membranipora crustulenta		×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Nereis diversicolor			×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
*Idothea viridis**					O	O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
*Calliopius laeviusculus**					O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	Only in saline water
*Praunus inermis**					O	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Gobius flavescens					×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
— *minutus*					×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	

O: Personal observations in rock-pools. × : According to information taken from the literature. *: After the name of the species indicates that the statement of salinity in the right side is not based on a ‰ statement, but it is estimated after a local statement. Species which according to information exist in "brackish" water are stated at 2‰ with × in parenthesis.

Oxygen and Carbon Dioxide

Gas content of the water in tidepools is determined partially by biological processes of photosynthesis, respiration, and decomposition. In strong sunlight, photosynthesis may greatly increase the oxygen content and decrease the carbon dioxide content while respiration during the hours of darkness will result in an increase in carbon dioxide content and a decrease in oxygen content. Bacterial decomposition of organic debris may tend to produce an oxygen-minimal layer on the bottom. Pools with large algae populations will have higher oxygen content as well as higher hydrogen-ion content (greater acidity) (Lewis, 1964). Lewis graphically illustrated diurnal changes in oxygen content, comparing pools with different floral populations (Figure 13).

Shape of Pools, Exposure

Depth, size, surface to volume ratio, elevation on shore and type of substratum are important factors which will affect the structure and evolution of a tidepool community. In general, larger volume relative to surface area results in more uniform conditions (Hedgepeth, 1957). Large, deep pools that are located lower on the shore are usually more stable (Lewis, 1964).

Tidepools may afford protection from desiccation to certain plant and animal species and enable these species to extend further upshore. Tidepool communities develop slowly and are very sensitive to fouling by animals outside of the tidepool system as well as other kinds of pollution. Tidepools can be used as indicators of the quality of water bathing the shore and may also yield clues as to beach formation and destruction (Hedgepeth, 1957).

Migration of animals such as Littorina snails and fishes in and out of tidepools may influence the community in many ways. If such migrators are removing energy from the system and not contributing to the energy budget, this loss of energy may serve to decrease species diversity within the tidepool, as energy will be used for repair and reproduction rather than for diversification. Flushing out of organisms and nutrients by tides would also represent an energy loss to the tidepool community and may serve to decrease stability.

Johnson and Skutch (1928b) concluded that alternating exposure and submergence, as determined by tidal fluctuation, is the most important factor influencing tidepool communities. In their report on submersible plant communities in Maine tidepools, they stated that the only features of tidepools not directly dependent on tides are the type of substratum and the direction and degree of exposure of the pools to the sun.

Pool Elevation

One manner in which tidepools can be classified is by the shore level at which they are located--supralittoral, littoral and sublittoral (Hedgepeth, 1957). However, it is difficult to generalize about conditions at different levels because the size of the tidepool may be an overriding factor and the boundaries of the zones are hard to define. Small shallow pools will be more sensitive to insolation, air temperature and rainfall than larger

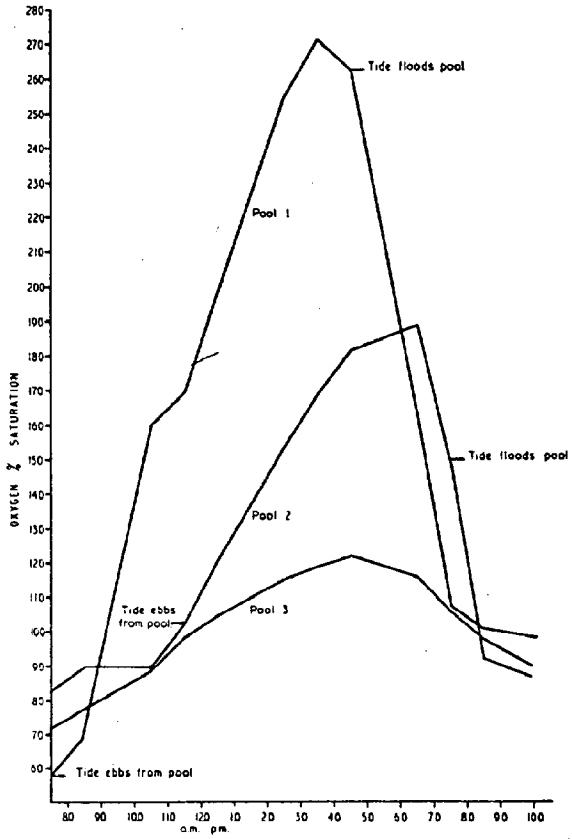


Fig. 13. Diurnal changes in O_2 content. Pools 1 and 2 occurred at the same level but 1 had a much denser flora than 2. Pool 3, above M.H.W.S., had a very sparse flora. Readings taken on different days. (From Pyefinch [102].)

Note changes in oxygen content relative to density of flora (Lewis, 1964).

pools that are at the same level. The size factor may cause different types of communities to develop in pools that are located at the same level. Consequently, littoral species might be found in a supralittoral-level tidepool (Lewis, 1964; Ricketts and Calvin, 1952).

Hedgepeth (1957) discussed general characteristics of tidepools at different levels on the shore. Supralittoral pools will probably be affected only by extreme tides and sometimes are more estuarine in character due to freshwater seepage. Littoral pools are the ones most similar to the sea, being covered at high tide and disconnected from the sea at low tide. Although sublittoral pools are characterized by a constantly varying surface level, these tidepools provide a quieter environment as compared to the sea.

Plant and Animal Life

Lewis (1964) discussed general characteristics of tidepool flora and fauna. He stated that the coralline algae Corallina officinalis, and Lithothamnia are most successful in shallow, well-lighted pools located at high levels on the shore, with estuarine species becoming dominant at the highest levels. Lewis stated that faunal elements are seldom found in profusion with the exception of sea anemones on Atlantic coasts and sea urchins on the Irish Coast. In tidepools along the west coast of Ireland, nearly all available space in shallow pools is often occupied by the purple sea urchin Paracentrotus lividus. Figure 8 shows shore zonation as well as the location of this type of tidepool on the west Irish Coast.

Lewis also observed that some rock species such as Corallina, Lithothamnia and the limpet Patella aspera seemed to be limited in range primarily by desiccation and were able to extend further upshore in tidepools. Other rock species, however, such as fucoids and barnacles, did not extend upshore in tidepools. Barnacles, in particular, were rarely found submerged. Only a few species seemed able to benefit from continued submersion in the tidepool environment.

Value as Microcosms for Research and Teaching

The study of tidepools as small marine microcosms can be a valuable learning experience for ecology students of all ages as illustrated by Bovbjerg and Glynn (1960). Organization, interaction and community structure on a small scale can be observed in tidepools, giving students an excellent opportunity to use their imaginations and knowledge in order to determine what factors are operational in the development and maintenance of the system. The student is made aware of the complexity of even small ecosystems and perhaps will be able to arrive at a feeling for the whole rather than merely an enumeration of the parts. As spots of particular interest and beauty, tidepools are important to the recreational value of the sea coast for man. Efforts should be made to protect these pools from pollution as well as from over-enthusiastic collecting in order that the maximum educational and recreational benefits may be obtained from them.

Stress and Diversity within Tidepools

A system may be defined as an organization of similar or diverse parts bound by a common goal or function and acted upon by common forces. Each member of a tidepool community is exposed to common forces such as chemical and physical changes related to oceanic and atmospheric conditions. Although these conditions may vary greatly from day to day, the summation of these forces can be regarded as a constant characteristic if considered over longer periods of time. Organisms living permanently in the tidepool community would have to adapt to a relatively unstable environment. Therefore, the inherent stress characteristic of tidepool communities would act as a common denominator and would unify the community into a working whole, that is, a system. The stress acting upon the tidepool system, as well as spatial limitations, would tend to decrease species diversity, with species using energy for repair rather than for diversification. However, the irregular substratum of some tidepools may tend to increase species diversity within the community.

Chapter C-2

BIRD AND MAMMAL ISLAND SUBSYSTEMS OF HIGHER LATITUDES

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Ten thousand and more animals living together on a rugged sea coast present an awesome spectacle to those fortunate enough to experience first-hand the noisy, dynamic subsystem characterized by bird and mammal islands. This subsystem is present on the rocky coasts of higher latitudes in the Pacific and Atlantic oceans. The bird and mammal islands are most abundant on the coast of Alaska. These systems need not be islands; they can be islands, rocks, or cliffs, but in most cases the animals seek protection from terrestrial predators and their colonies are typically on islands.

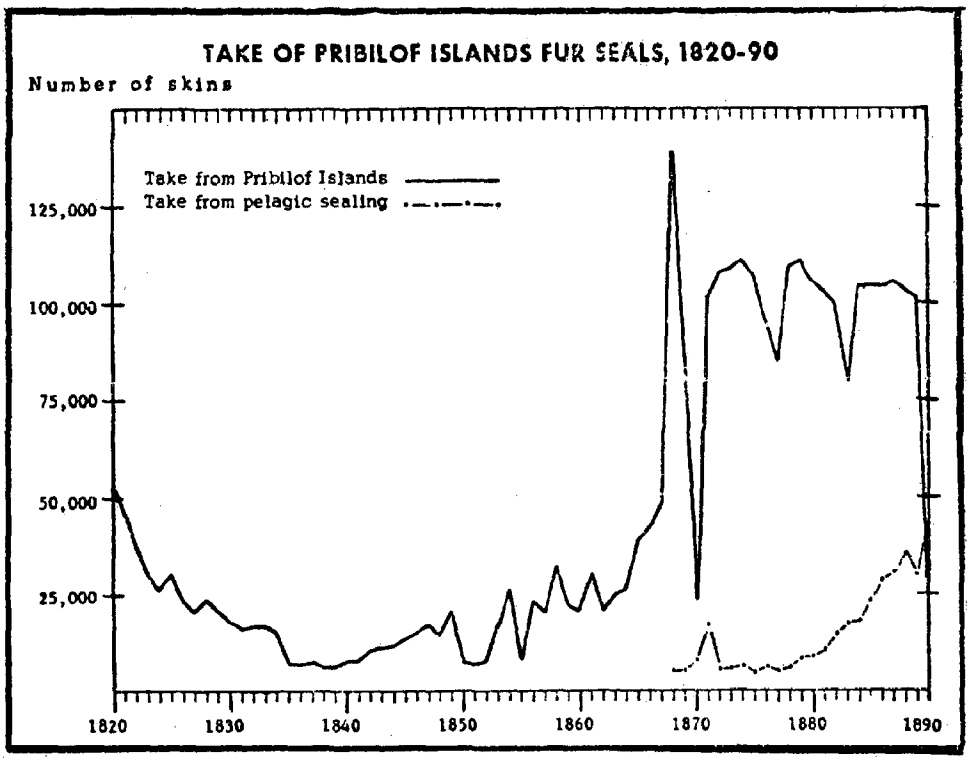
These systems are large breeding colonies of marine birds or mammals. Most of the species forming colonies are pelagic for eight or more months of the year and spend the remaining three or four months on the coast in a colony or rookery organized for the essential process of reproduction. These then are also migratory subsystems. The long northern winter months are spent at sea at the edge of the sea ice, farther south along the coast of California or Japan (for Pacific animals), or along this entire region (Tuck, 1960; Scheffer, 1958; Gabrielson and Lincoln, 1959).

EXAMPLES

Bird-mammal island subsystems that have been investigated include the Pribilof Islands and St. Lawrence Island, Alaska, in the Bering Sea; Cape Thompson, Alaska, in the Chukchi Sea; the Gulf of St. Lawrence and Newfoundland on the Atlantic coast of North America; and the coast of Alaska. Figures 1-10 illustrate the quantitative characteristics of some of these subsystems. Some illustrations of the marine mammals and their ranges are also included.

Distribution and Abundance

In the higher latitudes of the northern hemisphere there are 37 species of sea birds that nest in colonies (Table 1). Of these, 18 are restricted to the Pacific Ocean, 8 to the Atlantic Ocean, and 11 are common to both oceans. The most abundant of these birds and probably the most abundant birds in the Northern Hemisphere are the two species of murres (Thick-billed and Common); Tuck (1960) estimates these populations to be 50 to 100 million individuals. The largest breeding colonies of murres in the Pacific are on Bogoslof Island in the Aleutians and St. Paul, Walrus, and St. George islands in the Pribilofs. The murres on St. George alone number into the millions (Petersen and Fisher, 1955). Other sea birds in the more restricted regions are as abundant as murres. The dovekie in the North Atlantic and the least auklet in the North Pacific may exceed the numbers of murres in those regions (Tuck, 1960). The total number of sea birds on the coast of Alaska alone is immense and perhaps exceeds 200 million, certainly not less than 100 million.



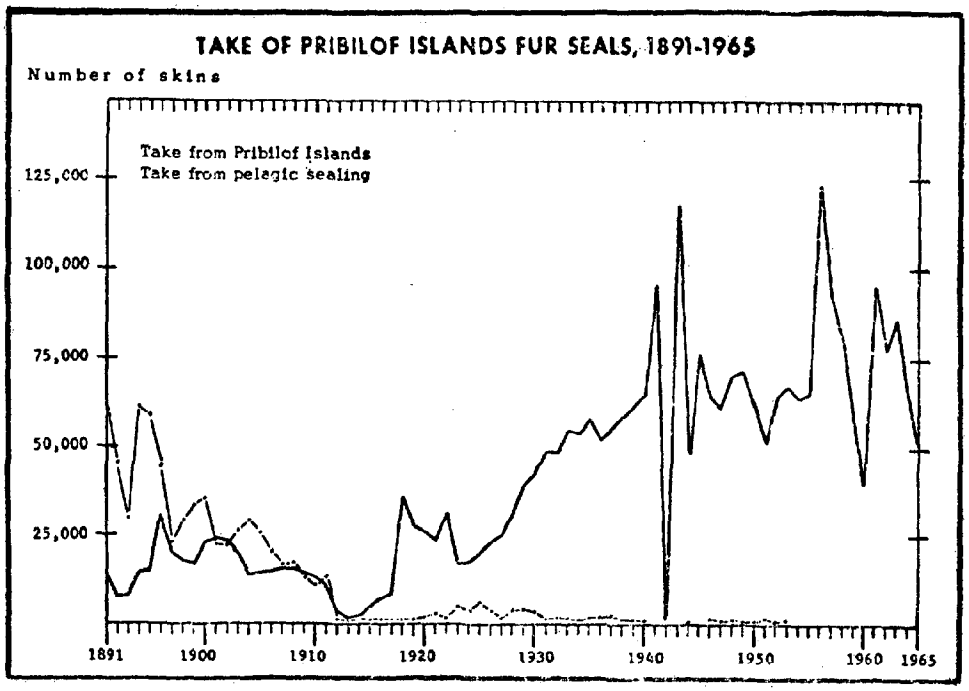


Fig. 1. Harvest of fur seals from the Pribilof Islands for 1820-1965 (From Riley, 1967).

Table 1. Sea birds that form nesting colonies in higher latitudes of the Northern Hemisphere (from Petersen, 1958).

I. Pacific Ocean Species

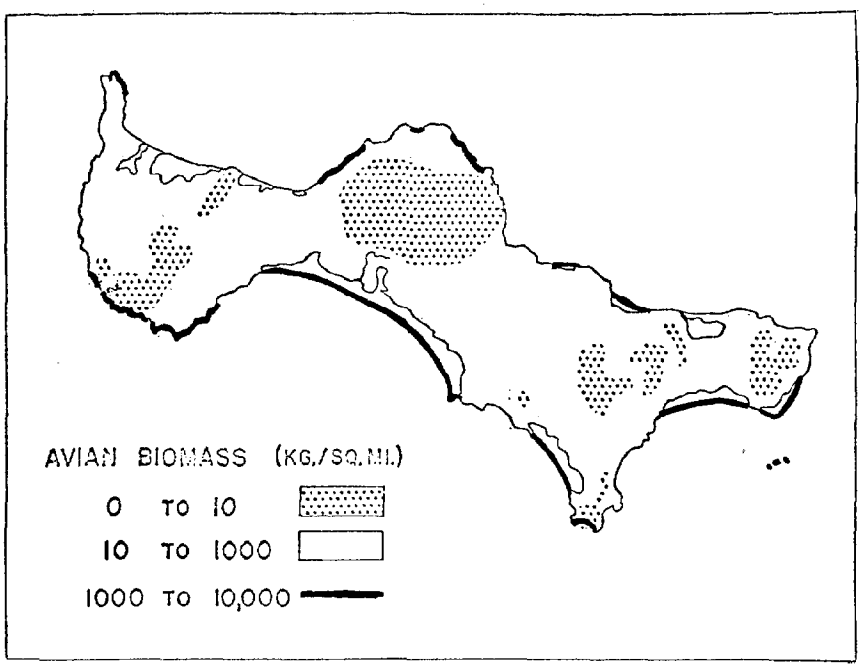
Pelagic Cormorant *(Phalacrocorax pelagicus)*
Red Faced Cormorant *(Phalacrocorax urile)*
Glaucous-winged Gull *(Larus glaucescens)*
Red-legged Kittiwake *(Rissa brevirostris)*
Pigeon Guillemot *(Cepphus columba)*
Marbled Murrelet *(Brachyramphus marmoratum)*
Kittlitz's Murrelet *(Brachyramphus brevirostre)*
Ancient Murrelet *(Synthliboramphus antiquum)*
Cassins Auklet *(Ptychoramphus aleutica)*
Parakeet Auklet *(Cyclorrhynchus psittacula)*
Crested Auklet *(Aethia cristatella)*
Least Auklet *(Aethia pusilla)*
Whiskered Auklet *(Aethia pygmaea)*
Fork-tailed Petrel *(Oceanodroma furcata)*
Rhinoceros Auklet *(Cerorhinca monocerata)*
Horned Puffin *(Fratercula corniculata)*
Tufted Puffin *(Lunda cirrhata)*
Aleutian Tern *(Sterna aleutica)*

II. Atlantic Ocean Species

Dovekie *(Plautus alle)*
Razorbilled Auk *(Alca torda)*
Atlantic Puffin *(Fratercula arctica)*
Green Cormorant *(Phalacrocorax aristotelis)*
Great Black Backed Gull *(Larus marinus)*
Black Guillemot *(Cepphus grylle)*
Gannet *(Sula bassana)*
Iceland Gull *(Larus glaucoides)*

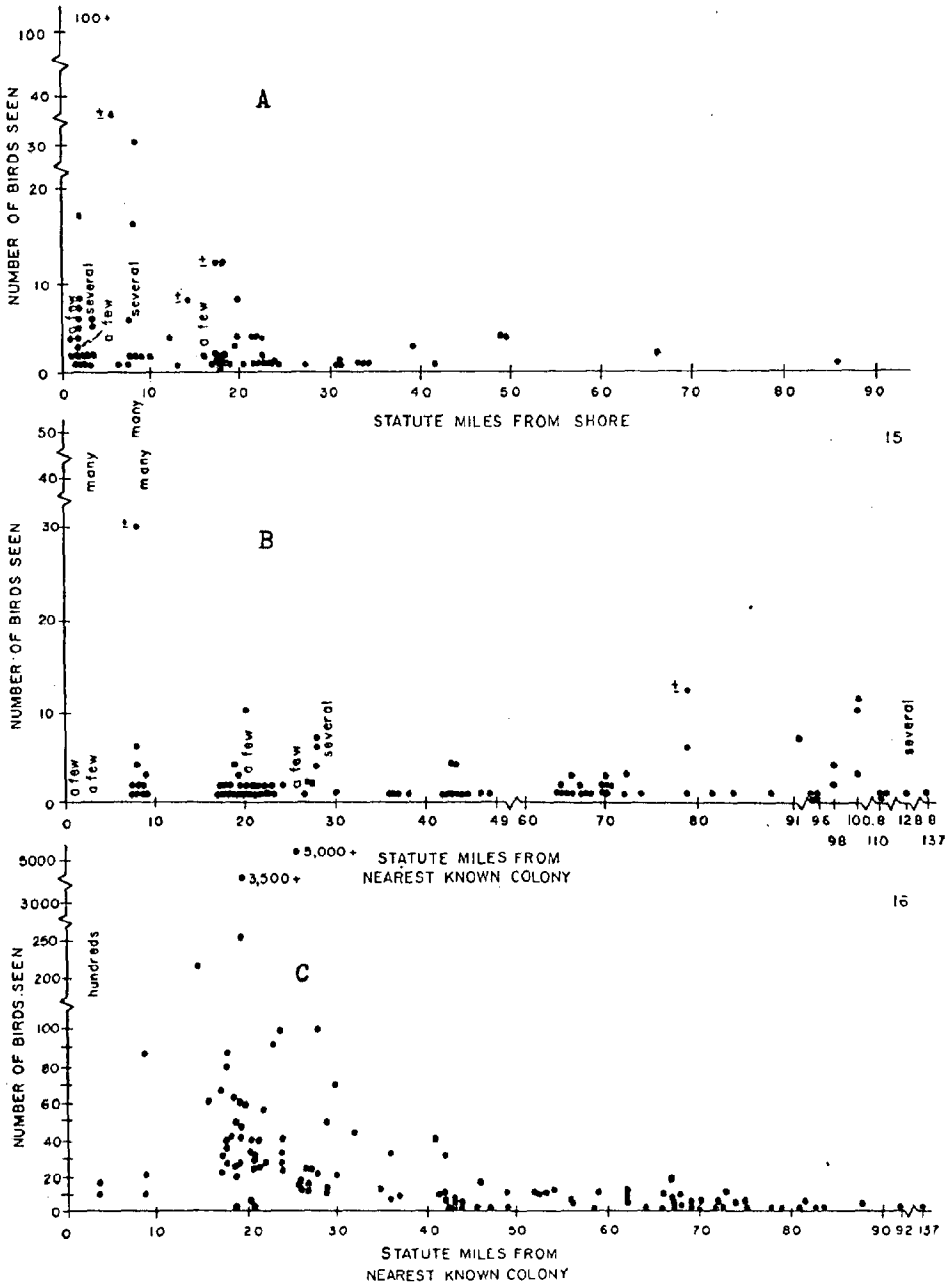
III. Circumpolar Species

Fulmar *(Fulmarus glacialis)*
Double crested Cormorant *(Phalacrocorax auritus)*
Glaucous Gull *(Larus hyperboreus)*
Common Murre *(Uria aalge)*
Thick-billed Murre *(Uria lomvia)*
Leach's Petrel *(Oceanodroma leucorhoa)*
Black-legged Kittiwake *(Rissa tridactyla)*
Ivory Gull *(Pagophila eburnea)*
Herring Gull *(Larus argentatus)*
Arctic Tern *(Sterna paradisaea)*
Common Eider *(Somateria mollissima)*



The distribution of avian biomass on St. Lawrence Island.

Fig. 2. Biomass of birds on St. Lawrence Island in 1957 (From Fay and Cade, 1959). The highest biomass zones along the coast are seacliff nesting colonies of murres, auklets, puffins, guillemots, kittiwakes, cormorants, and gulls.

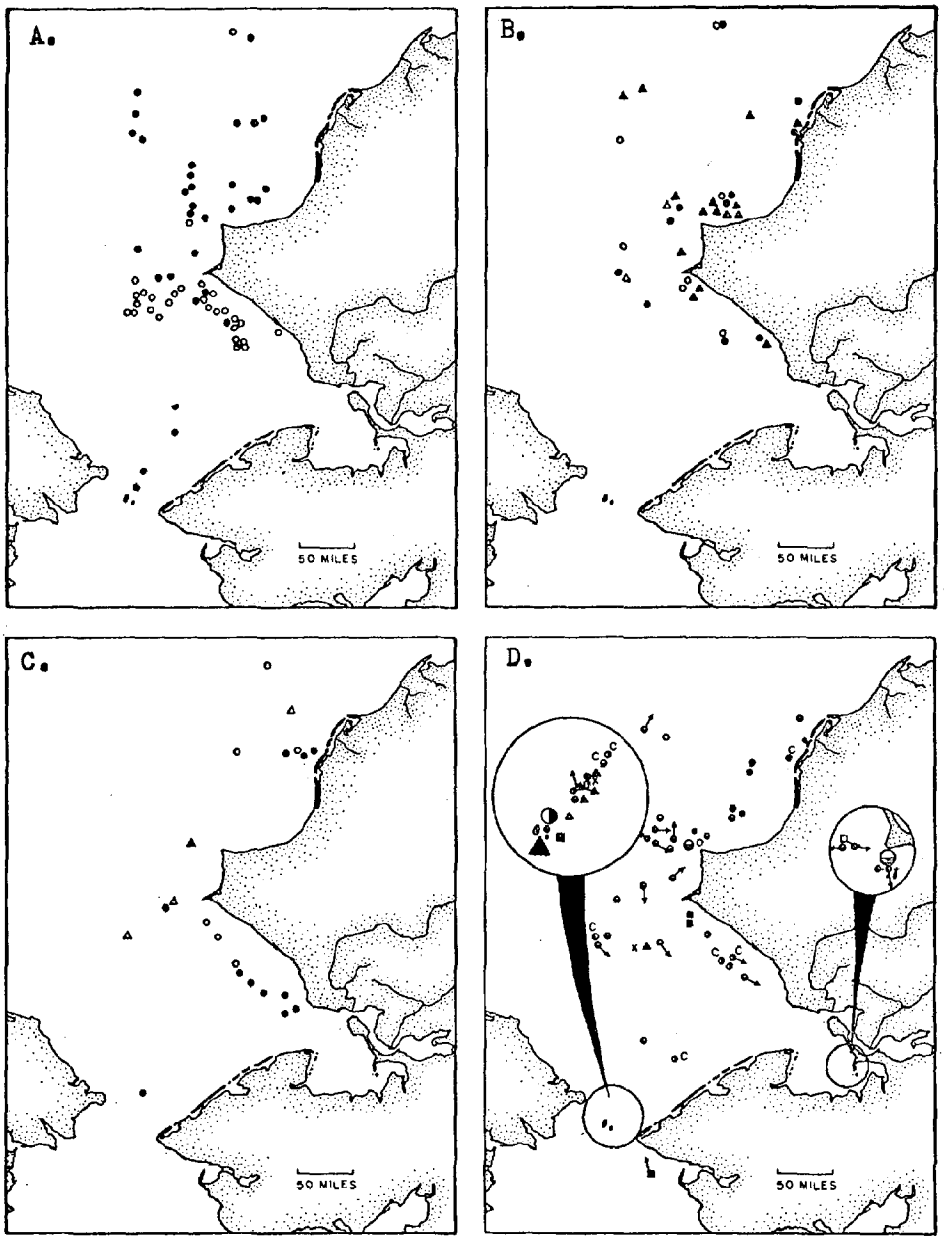


A Abundance of Glaucous Gulls vs. distance from the nearest shore. Since Glaucous Gulls may nest at many points along the shore, comparison is made between abundance and distance from the nearest land. All entries are included.

B Abundance of Black-legged Kittiwakes vs. distance from the nearest known colony Because of incomplete knowledge of nesting colonies, observations from 10-minute counts near and in Kotzebue Sound are not included. All other observations are plotted.

C Abundance of murres vs. distance from the nearest known colony. Due to the great amount of data available, only 10-minute counts are plotted. Because of incomplete knowledge of nesting colonies, data from 10-minute counts in and near Kotzebue Sound are omitted.

Fig. 3. The distribution of sea birds in the Chukchi Sea in relation to known nesting colonies (From Swartz, 1967).



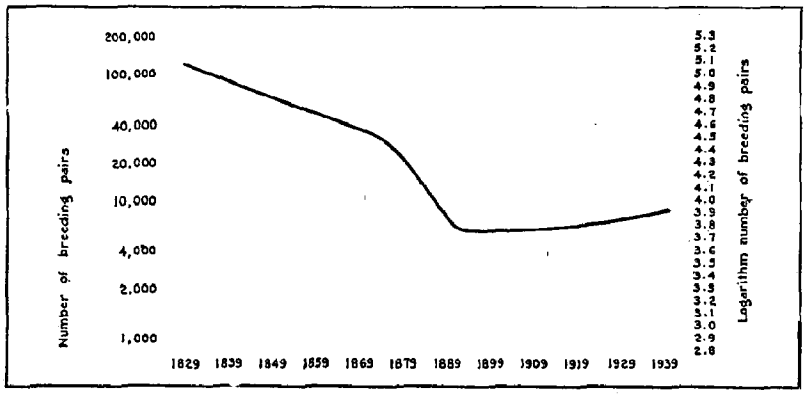
A. Observations of the Red Phalarope, ○; and unidentified phalaropes, ●

B. Observations of the Pomarine Jaeger, ○; Parasitic Jaeger, ●; Long-tailed Jaeger, △; and unidentified jaegers, ▲

C. Observations of the Sabine's Gull, ○; Arctic Tern, ●; Yellow Wagtail, △; and the Water Pipit, ▲.

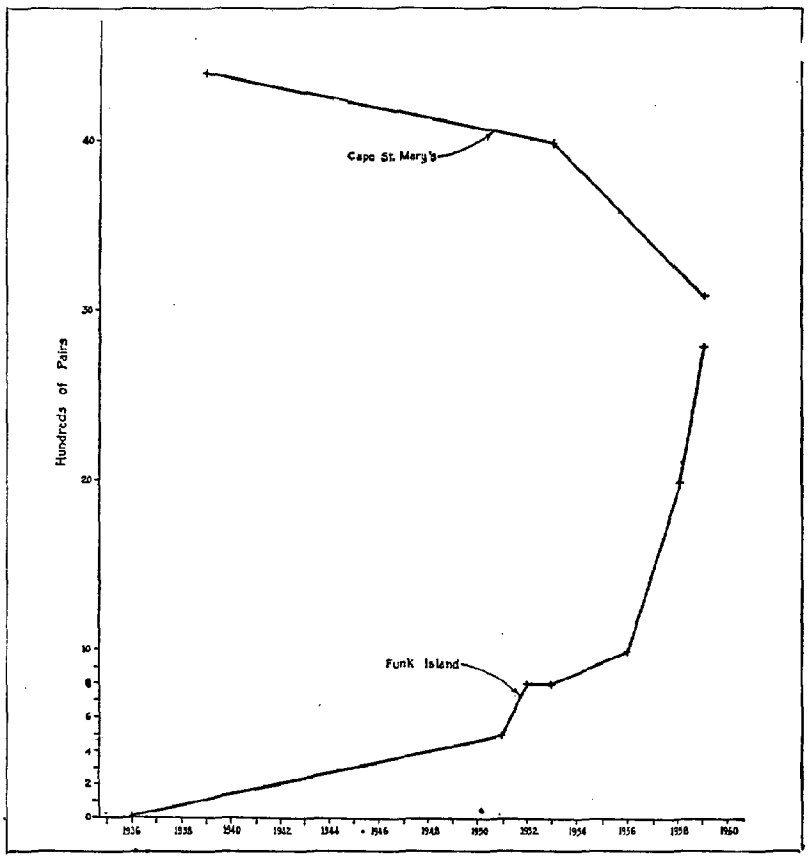
D. Abundance, distribution, and movements of the Pigeon Guillemot, ○; Kittlitz's Murrelet, ●; Parakeet Auklet, □; Crested Auklet, ■; Least Auklet, △; unidentified auklet, ▲; Horned Puffin, ◒; and Tufted Puffin, ◑ Numbers and direction of flight in both species of puffins is indicated by size of symbol and direction of vector: o, 1–5; ○, "some"; ◯, hundreds. *C* indicates the birds were circling.

Fig. 4. Observations and movements of birds in the vicinity of Cape Thompson, Alaska (From Swartz, 1967).



Changes in breeding populations of gannets in the Gulf of St. Lawrence, 1829-1939 (from Fisher and Vevers, 1944)

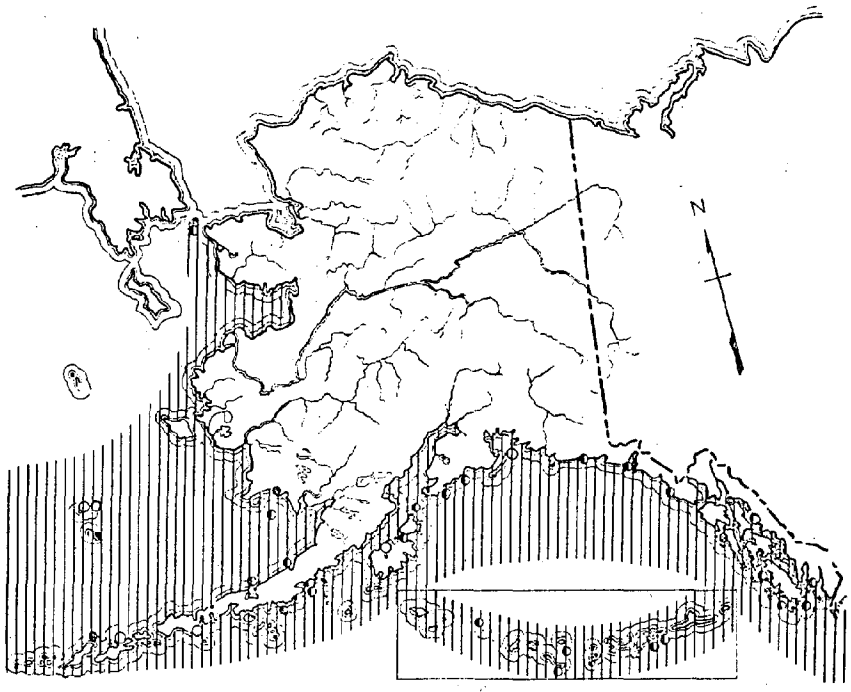
Fig. 5. Trends in breeding colonies of gannets in the Gulf of St. Lawrence, Atlantic coast (From Tuck, 1960).



Changes in breeding populations of gannets at Cape St. Mary's and Funk Island, Newfoundland, 1936-59

Fig. 6. Trends in breeding colonies of gannets in Newfoundland (From Tuck, 1960).

NORTHERN or STELLER SEA LION, *Eumetopias jubata*
(Urgak)



Range.—Bering Sea, Hall Island and Pribilof Islands, and Bristol Bay north to Bering Strait and south to islands off southern California.

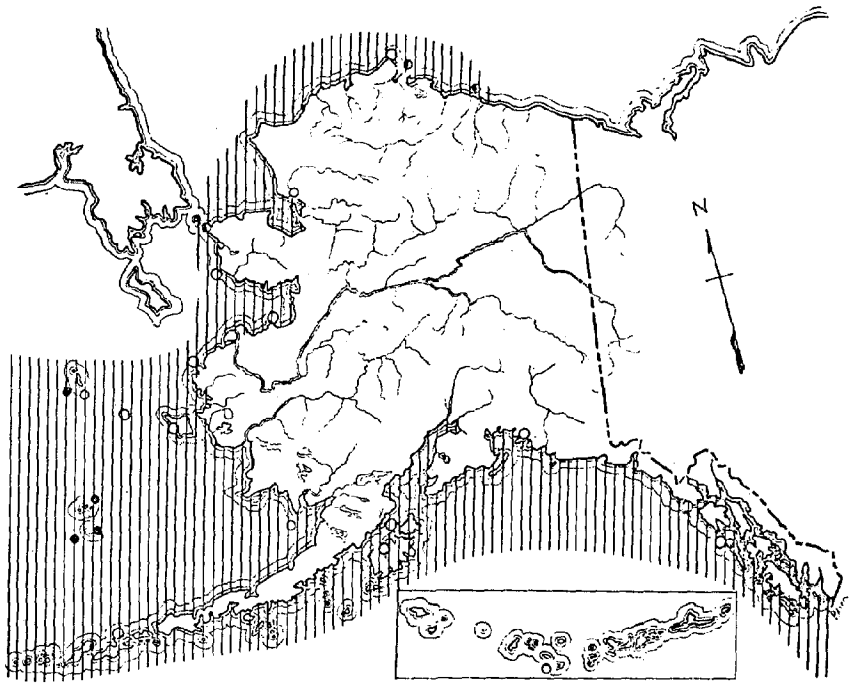
Habitat.—Marine, usually along open seacoasts; breeds on shore throughout most of its range.

Form in Alaska.—This is a monotypic species (type locality: "North Pacific Ocean").

Fig. 7. Range of the Steller sea lion in Alaska waters (From Manville and Young, 1965).

ALASKA FUR SEAL, *Callorhinus ursinus*

(Hlakudak)



Range.—North Pacific Ocean and adjacent seas breeds on Pribilof and Kurile Islands; occur casually north to a point east of Point Barrow

Habitat.—Marine; breeds on shores of islands pelagic and migrates south in winter.

Race in Alaska.—The race in Alaskan waters i *cynocephalus* (type locality: south of Alask Peninsula approximately at lat. 53° N., long 155° W.).

Fig. 8. Range of the fur seal in Alaska waters (From Manville and Young, 1965).

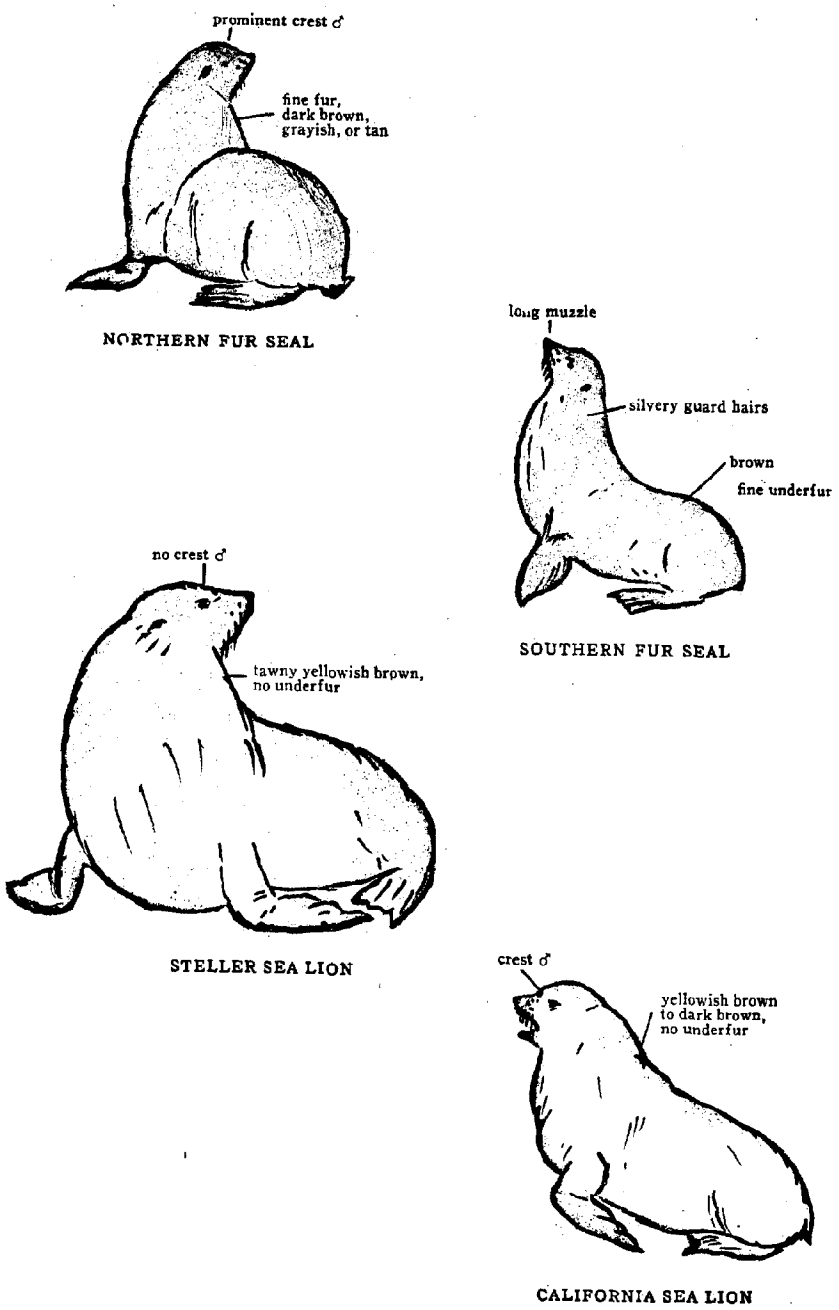
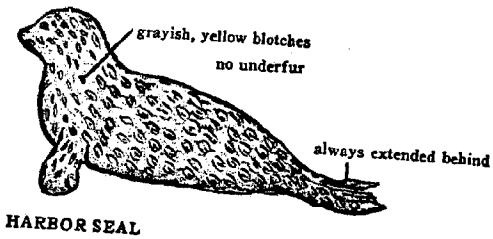
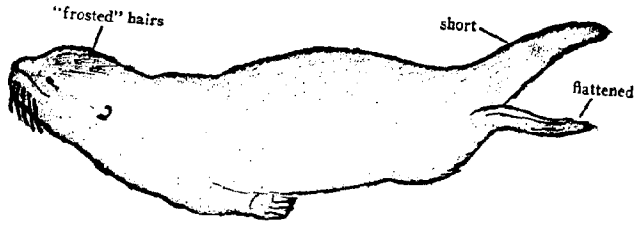


Fig. 9. Some marine mammals of the North Pacific: the northern fur seal, southern fur seal, Steller sea lion, and California sea lion (From Ingles, 1965).



HARBOR SEAL



SEA OTTER

Fig. 10. The harbor seal and the sea otter, marine mammals of the North Pacific (From Ingles, 1965).

Nine species of seals, sea lions, and walruses (pinnipeds) roam the high latitude seas of the Northern Hemisphere. The majority of these are circumpolar arctic animals associated with the sea ice for all their life activities. In seas with seasonal ice, the animals become pelagic during summer or follow the ice into the central arctic. This discussion is concerned only with the animals that breed in colonies on land. In the Pacific Ocean (North Pacific and Bering Sea), there are two species of these animals,

the Steller sea lion and the northern fur seal; the Atlantic has only one that might be considered in this category, the grey seal; and the one land-breeding species found in both oceans is the harbor seal (Table 2).

In lower latitudes of the Pacific North American coast live three other pinnipeds - the California sea lion (the circus seal, Zalophus californianus), the northern elephant seal (Mirounga angustirostris), and occasionally the southern fur seal (Arctocephalus townsendi) (Ingles, 1965). The sea otter (Enhydra luteus), a very different and relatively rare marine mammal, has only a few similarities to the pinnipeds. The sea otter is a mustelid, a relative of weasels, minks, and otters. Sea otters once ranged along the coasts of North America from California to Alaska. Currently a small population exists near Carmel, California, but most animals occur on the Alaska Peninsula and in the Aleutian Islands. The largest population lives on Amchitka Island in the Aleutians. Sea otters breed on rocky coasts but do not form the social, gregarious colonies typical of the pinnipeds (Murie, 1959). The young are born in the water.

The most abundant of the land-breeding marine mammals, the northern fur seal, is estimated to number 1.5 to 1.8 million (Table 2). The total population of marine mammals in Alaska can be estimated to be between 2 to 2.5 million.

Food Webs and Feeding Habits

These birds and mammals are links in marine food webs. They are in many cases direct links to food webs of terrestrial predators, including man (Fig. 11). The main food items are zooplankton, benthic and pelagic invertebrates, and fishes; a few animals occasionally sample the seaweeds (Taylor et al., 1955; Mathisen et al., 1962; Belopolski, 1957; Tuck, 1960). During the summer food is collected from areas near the coast in all directions from the breeding colonies. Sea birds may forage 20 to more than 100 miles from their breeding colonies (Belopolski, 1957; Figs. 12 and 13). The northern fur seal seeks food within a 150 mile radius of the rookeries (Baker, 1957; Fig. 14). Birds and mammals, through the process of food collection, can transport and concentrate organic material and nutrients independent of oceanic circulation.

The excretory and other activities of the animals result in the concentration of nutrients in the vicinity of the colony. This can have some positive feedback value for the breeding populations, since increased production in the surrounding waters should result. These animals will then not need to travel as far to collect the required quantity of food: energy will be conserved and may be channeled into the reproductive process.

The gregarious habits of the birds and mammals appear to be essential to this sort of feedback mechanism. Only through a large population can the rate of return of nutrients keep up with the dilution by tides and oceanic circulation. This nutrient enhancement is a feature of the high latitudes rather than tropical and subtropical regions. In low latitudes sea birds continuously remove nutrients from the system; these accumulate on land and are not returned, since the breeding colonies are in a region of little or no rainfall. These low latitude colonies must then be located near an area

Table 2. Marine mammals (pinnipeds) that breed in colonies on land in higher latitudes of the Northern Hemisphere (Scheffer, 1958).

	Estimated Abundance (individuals)
I. Pacific Ocean Species	
Steller Sea Lion *(Eumetopias jubata)*	60,000 to 150,000
Northern Fur Seal *(Callorhinus ursinus)*	1,500,000 to 1,800,000
II. Atlantic Ocean Species	
Grey Seal *(Halichoerus grypus)*	25,000 to 50,000
III. Both Oceans	
Harbor Seal *(Phoca vitulina)*	
Eastern North Atlantic	40,000 to 100,000
Western North Atlantic	40,000 to 100,000
Hudson's Bay	500 to 1,000
West Coast of North America	50,000 to 200,000
Asia	20,000 to 50,000
Total	150,000 to 451,000

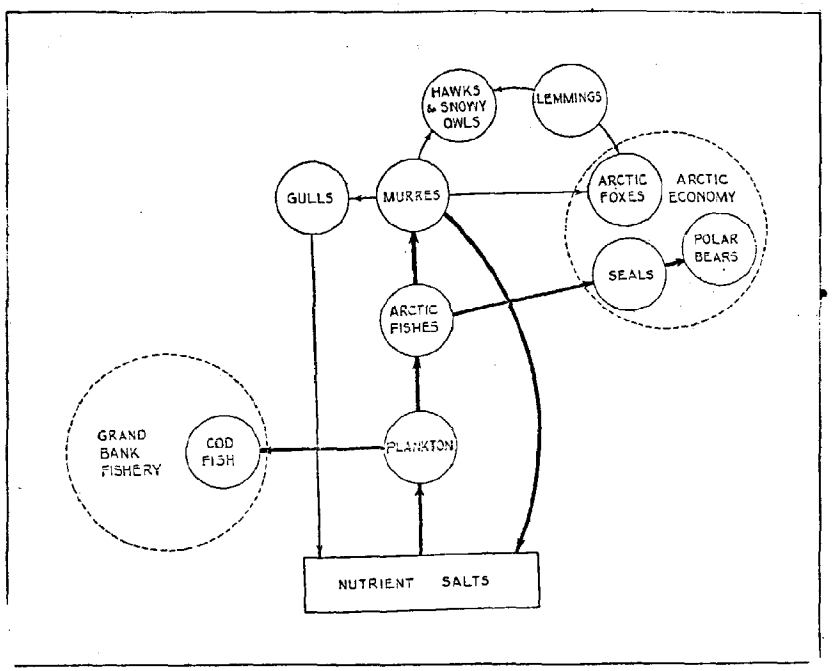


Fig. 11. Ecological relationships of murres (From Tuck, 1960).

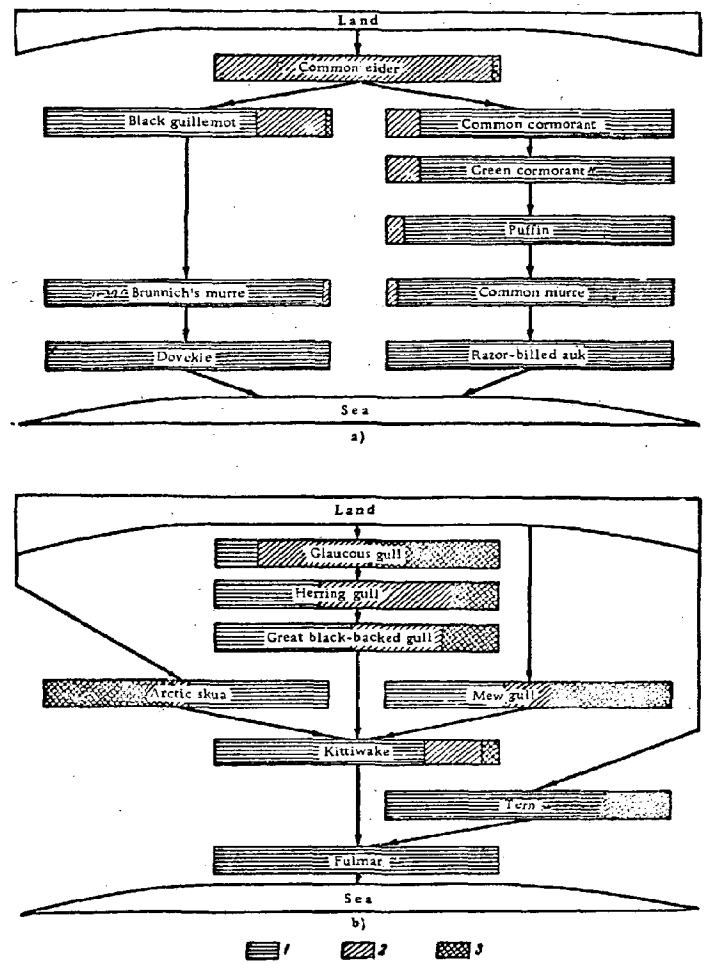


Fig. 12. Schematic distribution of diving sea birds (a) and non-diving birds (b) according to the character of their nutrition (After Belopolski, 1957). 1-pelagic foods; 2-littoral-coastal foods; 3-foods obtained on land.

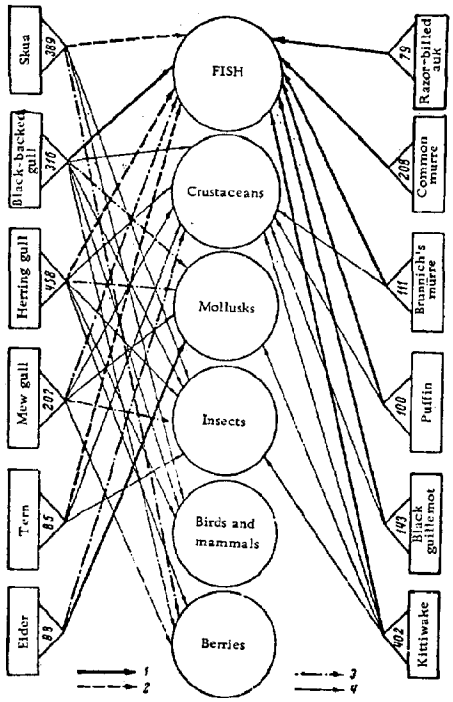


Fig. 13. Food webs of sea birds in the Barents Sea (from Belopolski, 1957).

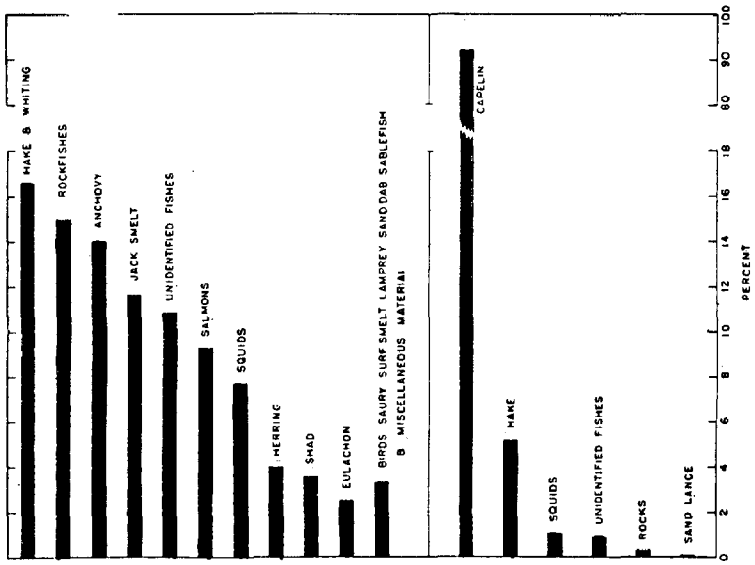


Fig. 14. Stomach contents of northern fur seals from the California-Washington-Oregon-Alaska coast (from Taylor *et al.*, 1955).

where a high ocean production is maintained by circulation mechanisms. Without the nutrients added by circulation, food would soon become scarce and the large populations of birds could not be maintained. For example, food for the great cormorant colonies of the Peruvian coast is maintained by the strong oceanic upwelling of the Humbolt Current that constantly replaces the nutrients for primary production (Dugdale and Goering, 1968). The cormorant colonies accumulate guano in the very arid climate; this guano is the basis of a commercial industry that is essentially removing nutrients from the local system. In the North Pacific and North Atlantic guano does not accumulate on the rocks of the colonies but the nutrients are continuously returned to the sea. These wet maritime climates are necessary to the maintenance of the colonies of sea birds and mammals.

Marine birds and mammals in turn fall prey to a variety of predators. Tuck (1960) could find no good evidence that any marine mammal in the Northern Hemisphere regularly, even irregularly, preys on sea birds. He suggests, though, that the killer whale may do so. Indeed, the killer whale is a well known hunter in the North Pacific; seals, especially the pups, are a principal item in his diet (Scammon, 1874). The heaviest predation on the sea birds occurs on young birds at the nesting colonies (Fisher and Lockley, 1954). The predators include eagles, hawks, falcons, the snowy owl, the raven, and several gulls. The glaucous gull in the Arctic lives in close association with the murre colonies and takes unattended eggs and chicks when the opportunity arises. Only two terrestrial mammals, the Arctic fox and the Norway rat, are important predators of sea bird colonies. Occasionally some fishes - halibut, cod, and sculpins - capture sea birds from the water.

Seals and sea lions are food for few predators (Allen, 1880). Other than the killer whale the only mammal that habitually hunts marine mammals is the polar bear, and this predation is restricted to the ice of the polar basin.

Man, of course, cannot be overlooked as a predator of sea birds and mammals. He is dealt with in the next section.

Storms at sea can impose additional mortality on all marine animals whose lives are bound to the air-sea interface. Mass mortalities of murre chicks from severe wind and rain have resulted on occasion (Tuck, 1960). Fierce storms may blow large flocks of sea birds inland to their doom. This is a frequent result of the Atlantic hurricanes and Pacific gales.

What controls the number of sea birds and marine mammals? The conclusion of Fisher and Lockley (1954) is that sea bird numbers are generally dependent on the size of the food supply. They present a convincing argument that the conditions of the environment that regulate the annual distribution, abundance, and availability of the food supply are the complex cog in the life history of most sea birds that controls their numbers.

The regulating mechanisms of the populations of the marine mammals are less known. Certainly in some species, such as the northern fur seal,

the harvest by man determines the size of the population. For other, non-commercial species, their numbers must again be related to the complex environment -food factor.

Economic Importance and Effects of Man

Sea birds are valuable aesthetic additions to the environment of man. Alaska annually draws many tourists from all over America to view undisturbed populations of birds and mammals; the more adventurous souls even visit the remote Aleutian, Pribilof, and St. Lawrence islands. Pacific coast states with bird and mammal colonies also attract many tourists. Similar visitors are lured to the Atlantic coast states.

Many sea birds and mammals are important food items to the native people of the north. Tuck (1960) calculated that nearly 2 million murre's eggs are used in the diet of northern natives annually. Cott (1953, 1954) showed that the eggs of the sea birds are the most utilized eggs of all wild birds. Many sea birds, especially murres, are annually taken for their flesh as well.

Nearly all marine mammals are hunted for food and hides by people indigenous to the north. The most valuable and well known resource is the northern fur seal, which is harvested on the Pribilof Islands in the Bering Sea. On the Pribilofs the annual harvest is now about 100,000 animals. These were taken only for their luxurious fur for many years, but in the last five years a by-product plant established on the islands has converted the seal carcasses to a high quality mink food. The value of the hides is about $5 million annually.

Sea lions are not harvested commercially to the extent of most other marine mammals. A limited harvest of sea lions occurs annually on the Alaska coast near Kodiak Island. The harbor seal is harvested along the coast by natives and at sea by ships of the Soviet Union (Burns and Kenyon, 1968). An experimental harvest of sea otter is now practiced by the Alaska Department of Fish and Game. The increased abundance of this fine fur animal has only recently permitted a limited harvest from the Amchitka Island herd.

Pollution of coastal waters presents critical problems to birds and mammals. The dumping of oil at sea has resulted in destruction of large numbers of sea birds. As early as 1926 an international conference was held in Washington to examine this problem, but still little has been done (Fisher and Lockley, 1954). Oil slicks on the sea surface are still a menace to sea birds and mammals. Oil reduces the insulation and buoyancy effects of fur and feathers and generally results in death of the animals. The recent "Torrey Canyon" disaster on the British coast killed thousands of sea birds (Smith, 1968). Similar smaller scale accidents have occurred in the past year in Cook Inlet, Alaska.

The coastal pollution poses the most serious threat these species have yet faced.

Research Needs

Knowlege of the functioning of marine bird and mammal island subsystems is deficient in many areas. For sound future management all of these need to be studied. The most important requirement is that research be environmentally and ecologically oriented rather than the more limited strictly zoological type of the past. This would involve defining nutrient and food cycles in relation to the dynamics of marine bird and mammal populations. The consequences of coastal pollution on marine bird and mammal subsystems must be understood. The gregarious habits of the animals leave not just portions of populations but entire species threatened with destruction. The effects of pesticides, oil, radioactivity, food processing plant wastes, and other pollutants need to be critically and thoroughly examined.

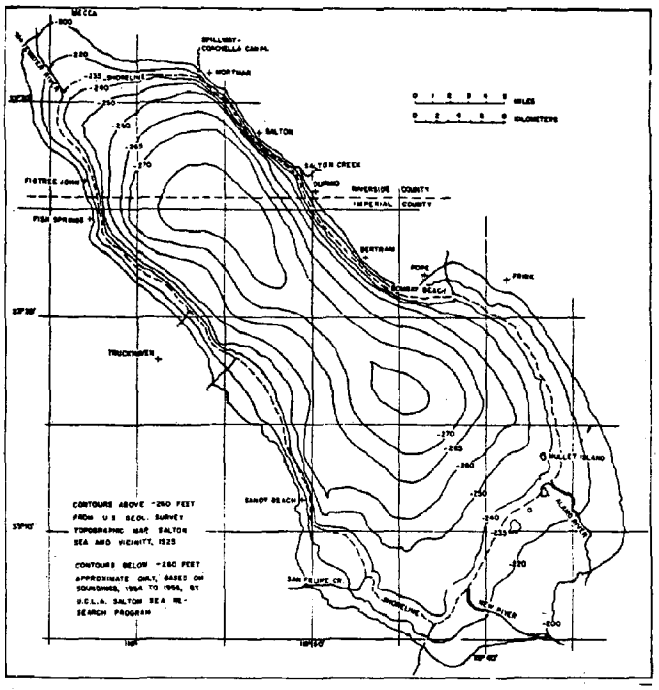
Chapter C-3

LANDLOCKED SEA WATERS

When waters are cut off from the sea or lakes develop salts similar to sea water, marine organisms may participate in ecosystems of the inland sea being physiologically adapted. However, such waters differ in major ways from the other estuarine systems. They do not have: appreciable tide, population pressure from more open waters, coupling to the seasonal pulse-migration-nursery pattern. Landlocked waters may be outside the scope of a coastal classification system, but proposals to cut off sea waters to form salty impoundments make these systems of interest.

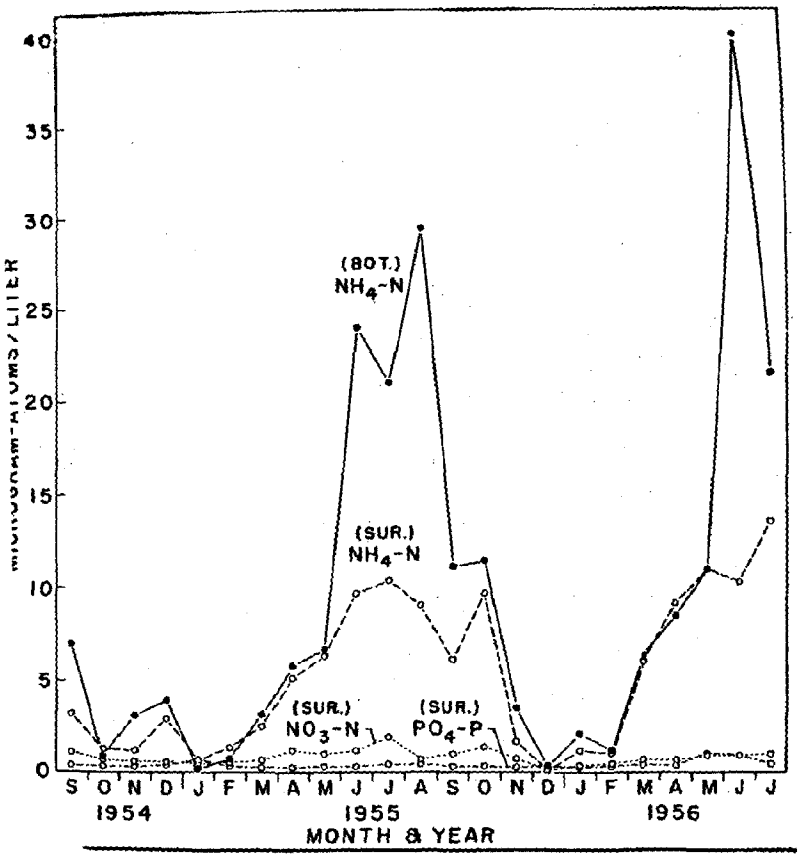
Examples

The Salton Sea in southern California (Fig. 1) refilling after a nearly dry period developed salinities like the sea with developing biological components many of which were stocked. The Caspian Sea is another often cited case which has marine species in landlocked pattern. The Salton Sea, California is shown in Fig. 1 and a few of the patterns of annual cycle given by Walker(1961) are given in Figs. 2and 3. That entirely new kinds of ecological systems can develop under partial management opens the door into a new promising era of ecological engineering.



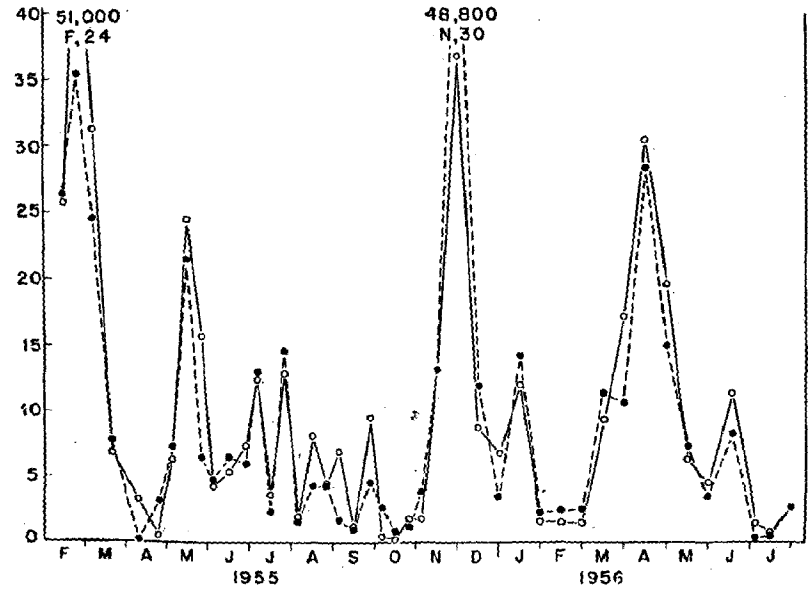
Depth contours of Salton Sea. Contours above —260 feet from U. S. Geological Survey, 1925. Contours below —260 feet are approximate only, based on soundings by U.C.L.A. Salton Sea Laboratory, 1954-1956.

Fig. 1. Landlocked sea waters of Salton Sea, California (Walker,1961).

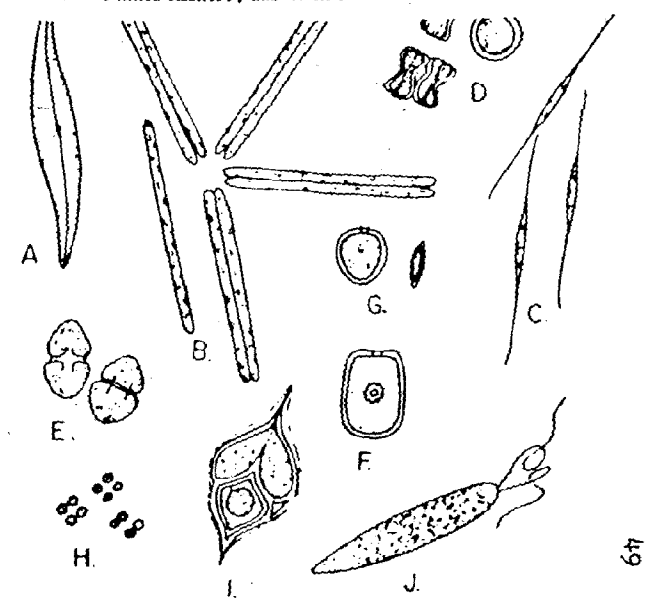


Ammonia-N, Nitrate-N, and Phosphate-P three miles off Fish Springs, Salton Sea.

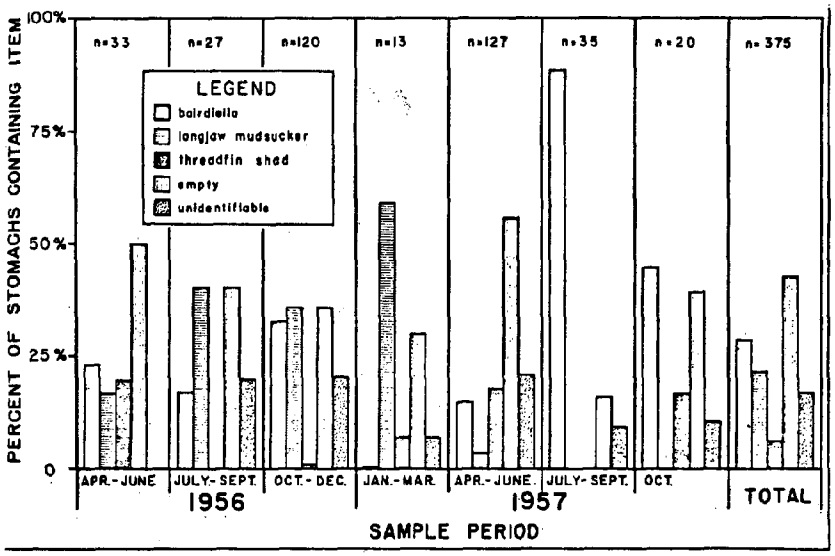
Fig. 2. Nutrients and phytoplankton producers in Salton Sea (Walker, 1961).



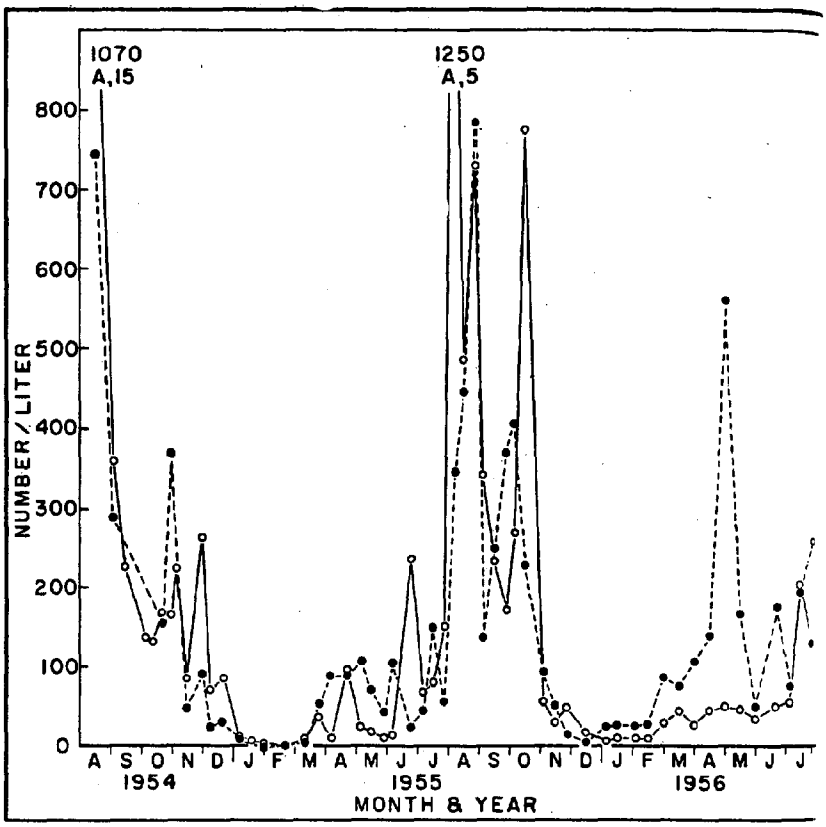
Total numbers of diatoms in individual collections, Salton Sea. Solid line = 3 miles offshore; dashed line = near shore.



Representative phytoplankton organisms of the Salton Sea. A. *Pleurosigma* sp., B. *Thalassionema nitzschoides*, C. *Nitzschia longissima*, D. *Cyclotella caspia*, E. *Glenodinium* sp. F. *Exuviella marina*, G. *Exuviella compressa*, H. *Westiella botryoides* (?), I. *Dictyocha* sp. (?), J. *Eutroptia lanowii*. Drawing by W. J. Baldwin



Relative percentages of various forage fishes in the stomachs of orange-mouth corvina from the Salton Sea. Since more than one species may have been present, the bars in some cases add to more than 100 percent. The high percentage of empty stomachs and unidentified fish remains were mainly due to the fact that the nets were usually set for 24 hours.



Total zooplankton in the Salton Sea, 1954-1956. Three miles offshore (solid line) and 100 yards from shore (dotted line). Offshore collections show average numbers for surface, mid-depth (six meters) and near bottom (12 meters). The near-shore stations show average numbers for surface and three meters.

Fig. 3. Zooplankton and food chain among fishes in Salton Sea (Walker, 1961).

Chapter C-4

THREE MARSH CHAPTERS

A marsh ecosystem includes both the emergent, grassy land zones and the tidal creeks that exchange salt waters. The cycles of mineral nutrients tie the land and water phases together, exports of one being the imports of the other. Often organisms form a controlling interface. For example, rich growths of plant cells such as diatoms grow on the surface of the rich black mud, emerging on the surface when the tide is out, but burrowing in when the waters cover the mud (Figs. 1-3). Ragotzkie and Pomeroy (1957) in Figure 4 show the history of a bloom of phytoplankton dinoflagellates as they shifted back and forth in a tidal creek in Georgia. In Cooper's Chapter C-4A, emphasis is on the land components of the marsh areas. Chapter C-4B by Diaber and his associates shows details of the aquatic biogeochemical cycling leading to productive growth of marsh in Delaware. Chapter C-4C by Marshall considers the rush marsh near the upper reach of the tide, a type that covers vast areas of the southeastern United States. Only occasionally inundated, it has mosquito populations at times. The marshes are a principal nursery for the critical rapid growth of many of the most valuable stocks of fishes and crustea. Figure 5 shows the seasonal periodicity of some species using the nursery during the spring and summer.

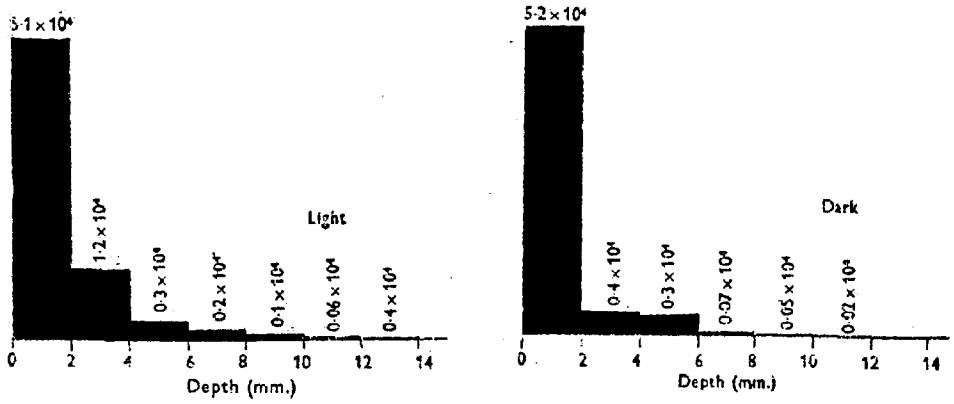
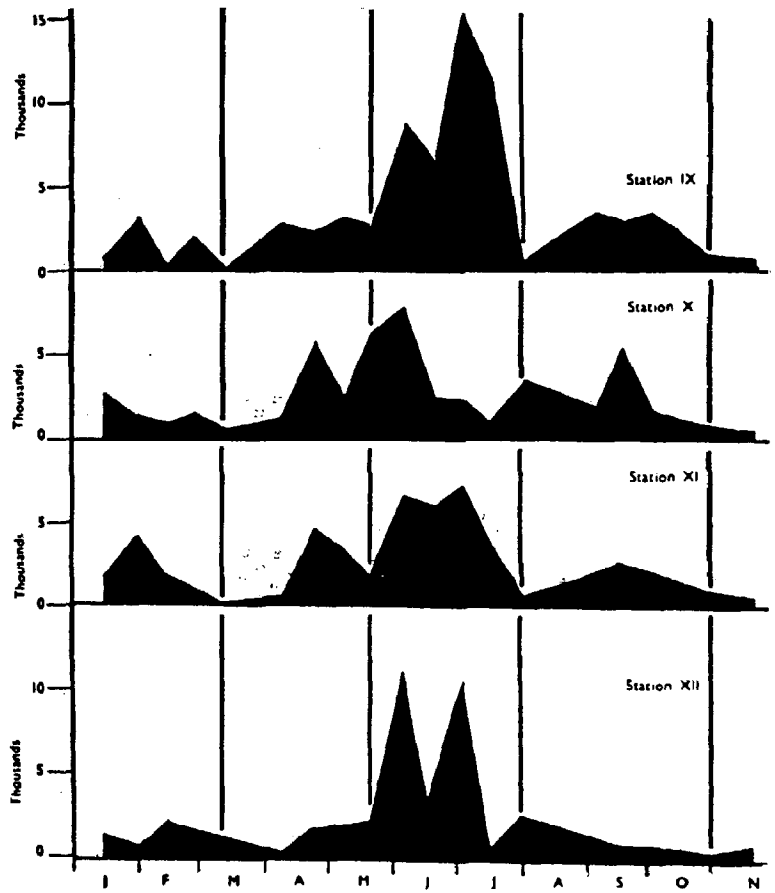
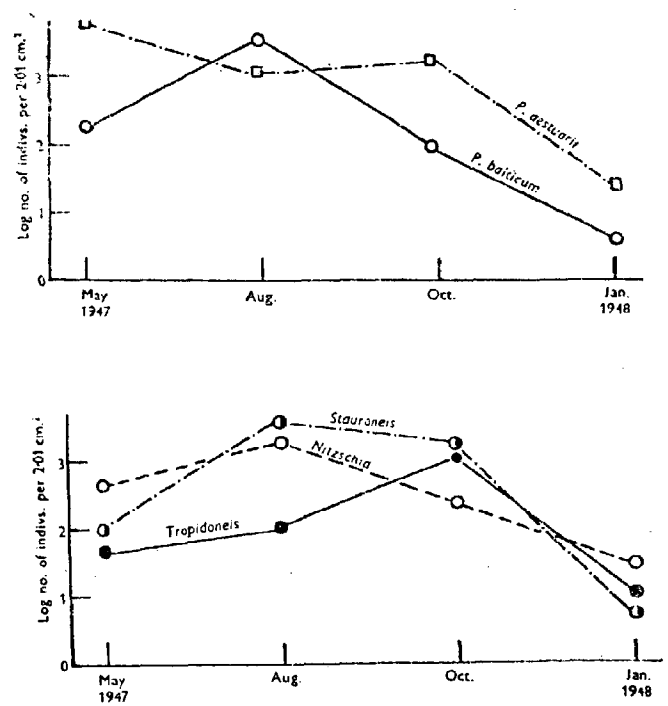


Fig. 1. Vertical distribution of burrowing mud diatoms. Histograms show the vertical distribution of the diatoms in a column of mud in the light and in the dark (Aleem, 1950)



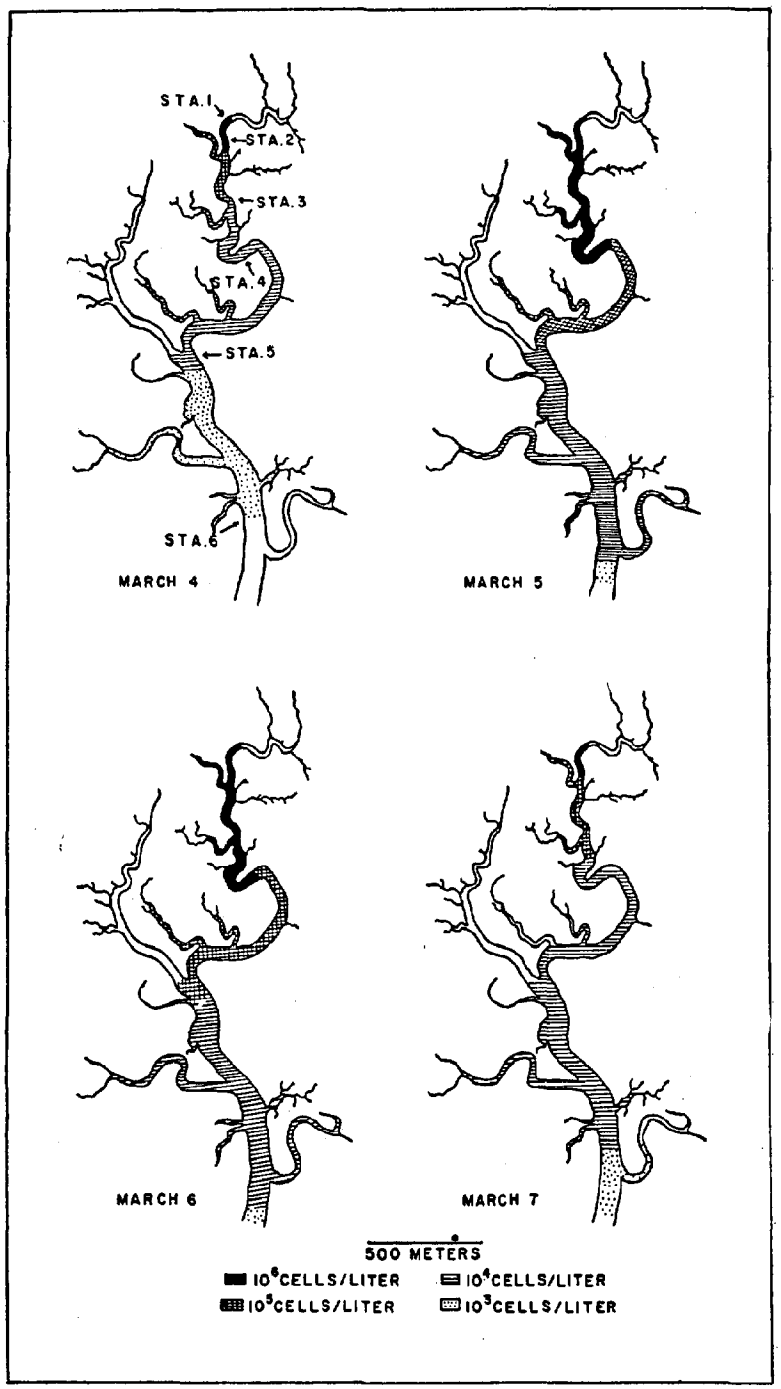
Seasonal cell counts of diatoms on the estuarine sand at four stations on the lower salt marsh at Neston, Cheshire. (From Round, 1960b.)

Fig. 2. Seasonal distribution of diatoms on salt marsh sands in England (Round, 1964).



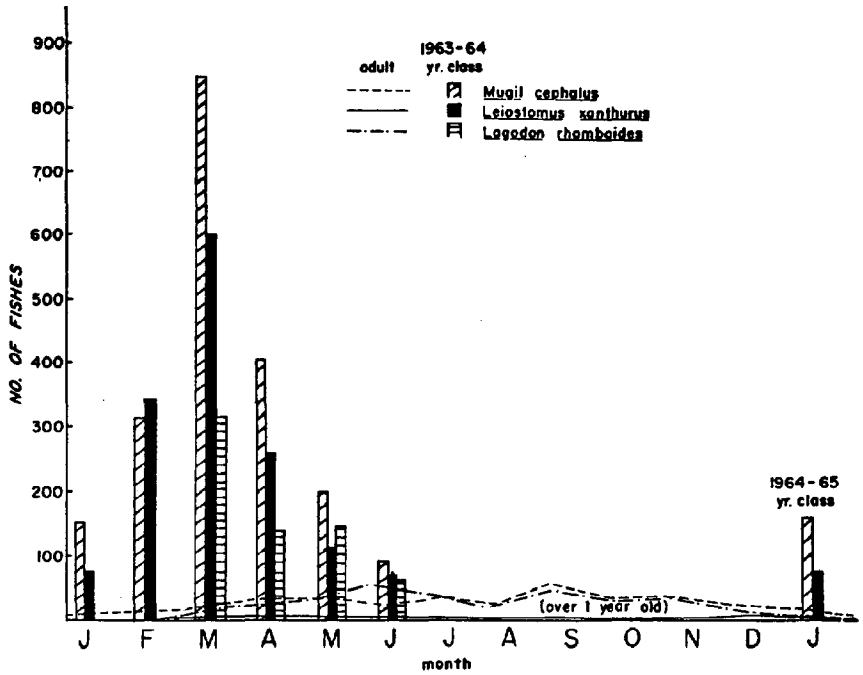
Seasonal periodicities of *Tropidoneis vitrae*, *Stauroneis salina* and *Nitzschia sigma*.

Fig. 3. Algal films on British salt marsh bottoms (Aleem, 1950).

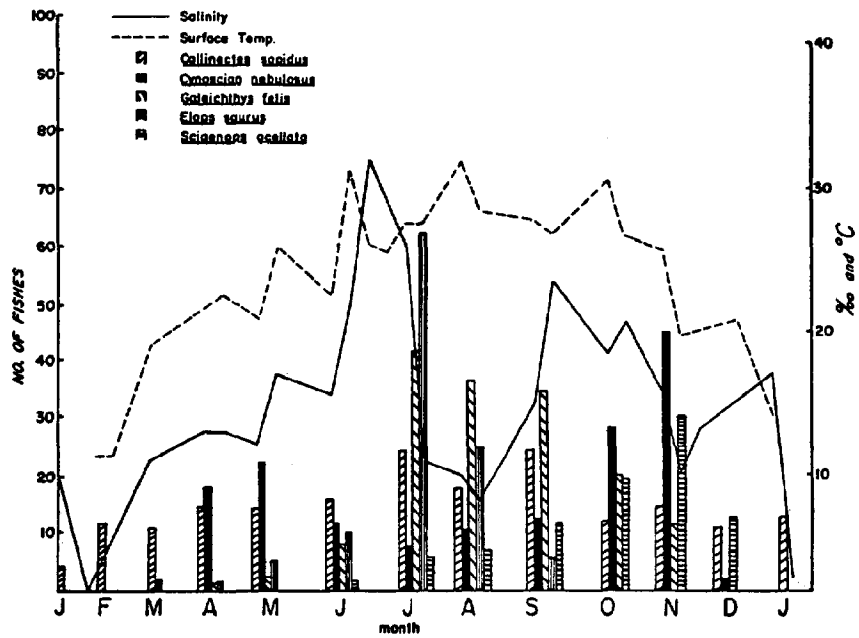


Distributions of *Gymnodinium* sp. in the upper 10-cm stratum of the Duplin River for 4–7 March 1955. The map of the river was drawn from an aerial photo mosaic made from official U. S. Navy aerial photographs. Both the mosaic and the photographs were supplied by the Glynco Naval Air Station, Brunswick, Georgia.

Fig. 4. Phytoplankton blooms in a tidal marsh creek in Georgia (Ragotzkie and Pomeroy, 1957).



Seasonal abundance of adult and juvenile *Leiostomus xanthurus*, *Mugil cephalus* and *Lagodon rhomboides* at Station 1.



Salinity, surface temperature and the abundance of the five main species of fishes at Station

Fig. 5. Seasonal patterns of fishes in a Florida marsh (Zilberberg, 1966).

Chapter C-4A

SALT MARSHES

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Raleigh, North Carolina

Salt marshes are beds of intertidal rooted vegetation which are alternatively inundated and drained by the rise and fall of the tide. As shown in Figures 1 and 2 (Shuster, 1966b) the vegetation on higher ground develops a complex network of branching water channels through which water, minerals, plankton, and fishes flow with the tides. The marsh ecosystem, thus, has above water components and aquatic organisms which are participants in one system of mineral cycles and food chains.

A salt marsh forms where plants invade shallow, relatively protected tidal flats. A salt marsh is typically intertidal, with much of its area alternately flooded and exposed on each tidal cycle. Consequently, salt marshes form in a tide-stressed environment which undergoes rapid diurnal change and in which several environmental factors, chiefly salinity, drainage, and temperature, exert a strong selective control over the kinds of species present. It is not at all uncommon for the plants and animals of a salt marsh to be exposed to salinities varying from 20-40 o/oo on a tidal cycle and this might be followed by a heavy rain shower dousing them with fresh water. Likewise, temperatures of the mud surface may vary over a range of 10 or more degrees C during the day. Some variations in a typical marsh environment are shown in Figure 3. The plants of a salt marsh must be able to tolerate these abrupt changes in environment whereas many of the animals have evolved mechanisms, such as burrowing, to avoid them.

Another important feature of the salt marsh is the intimate relationship which exists between the marsh and the adjacent waters of the estuary (Figures 1 and 2). Energy fixed in the marsh is washed out by the tide, in the form of tiny particles of organic matter (detritus). These form the food for many animals in the estuary. Other nutrients, such as phosphorus and nitrogen, are exchanged between the marsh and the estuary.

As a consequence of the rigorous environment of the salt marsh only a relatively small number of plants and animals are able to tolerate the conditions found there. Thus, it is not surprising that there is a rather high degree of similarity in the kinds of species present in United States salt marshes. Grasses of the genus Spartina and species of Juncus and Salicornia are almost universal in their occurrence, as are certain kinds of animals such as fiddler crabs and mussels. Despite this overall taxonomic similarity, certain species distributions combine with physiographic factors to produce several rather clearly defined marsh types in United States estuaries.

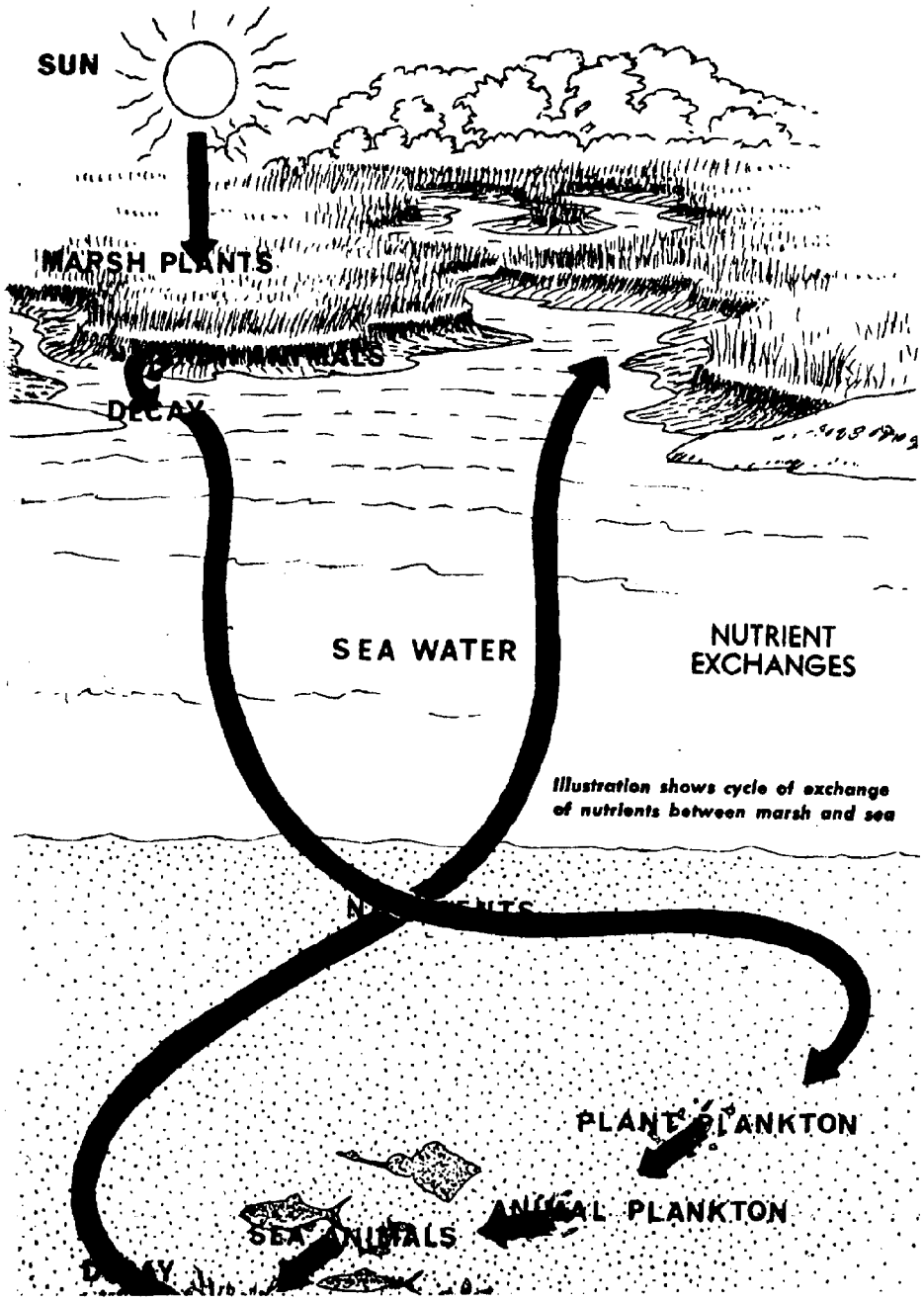


Fig 1. Exchange of nutrients between marsh and sea (from Shuster, 1966b).

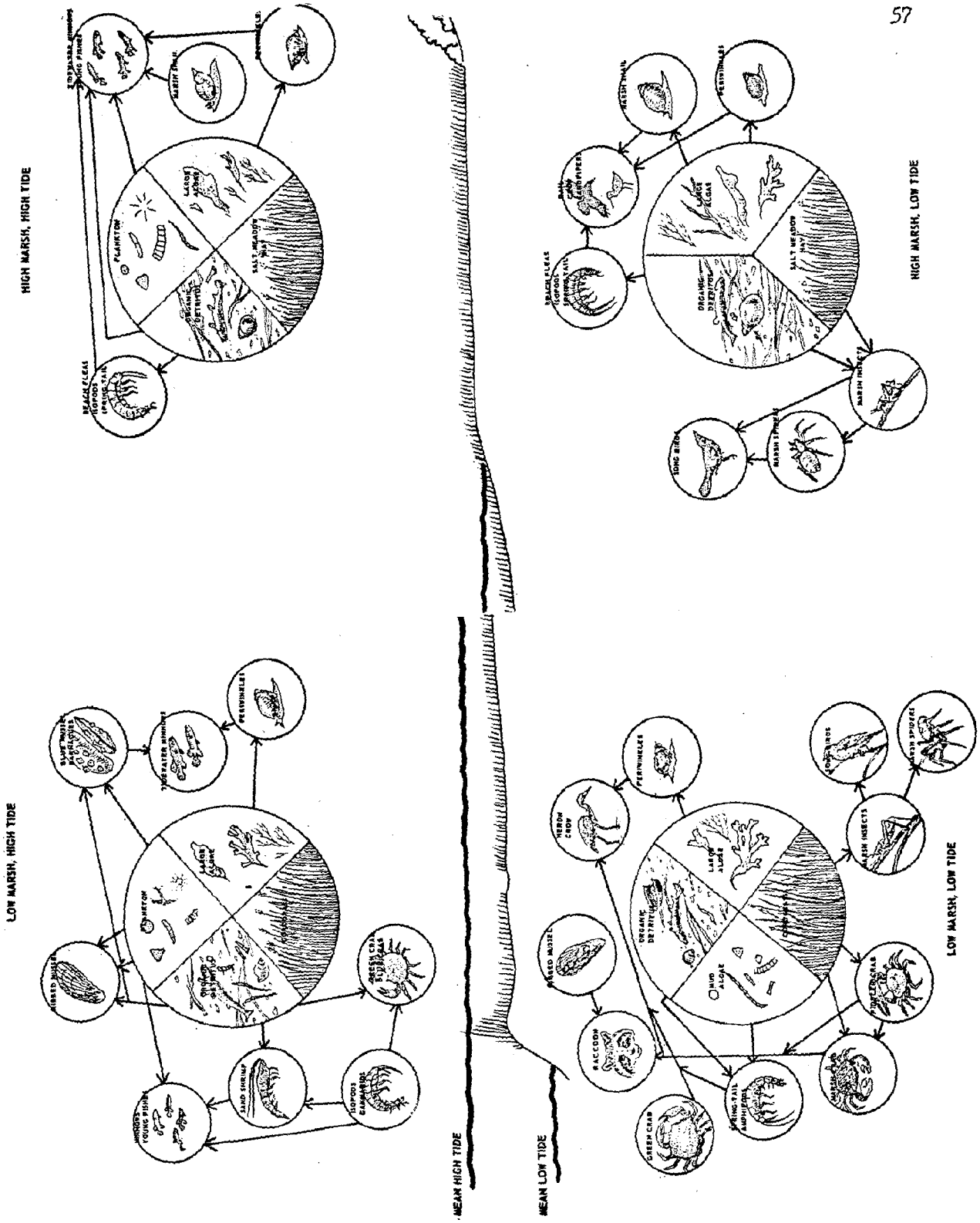
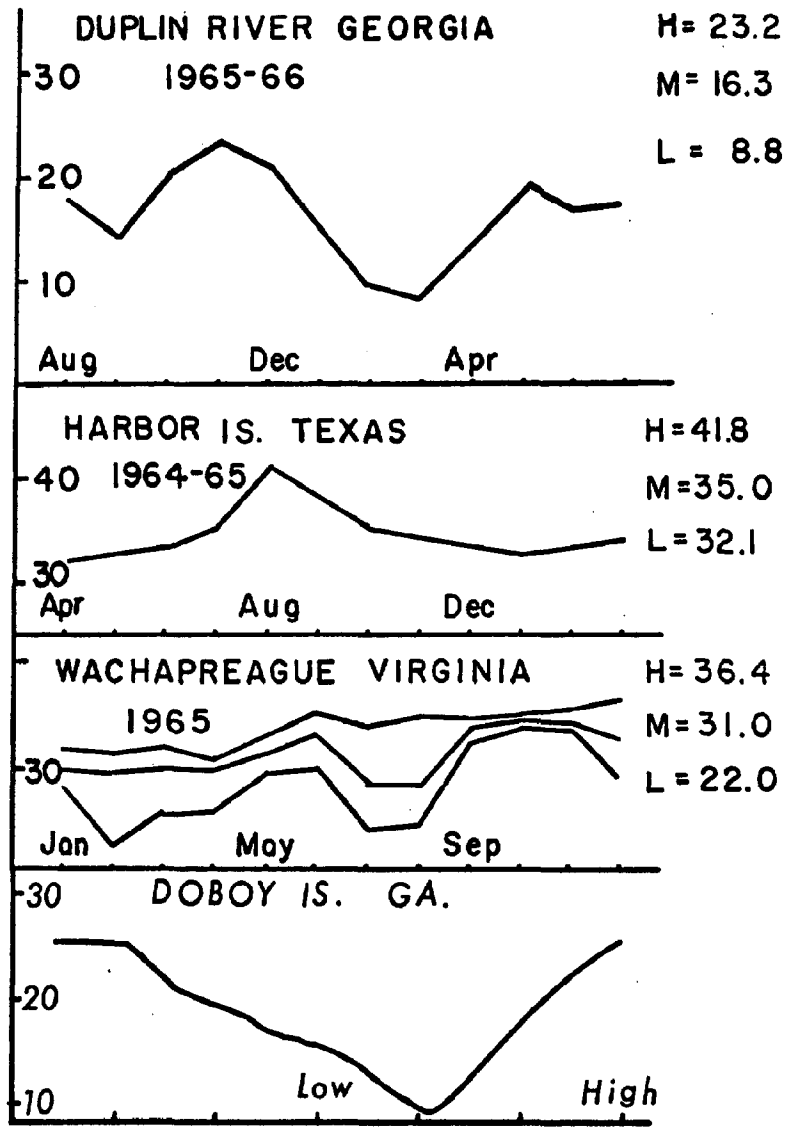


Fig. 2. Characteristic animals present in salt marsh at low and high tides and feeding interrelationships (Shuster, 1966b).



Seasonal salinities (ppt) in three salt marsh areas and tidal effect in one marsh (from Galtsoff and Luce 1930).

Fig. 3A. Salinity Records in salt marsh waters (Hoese, 1967).

EXAMPLE

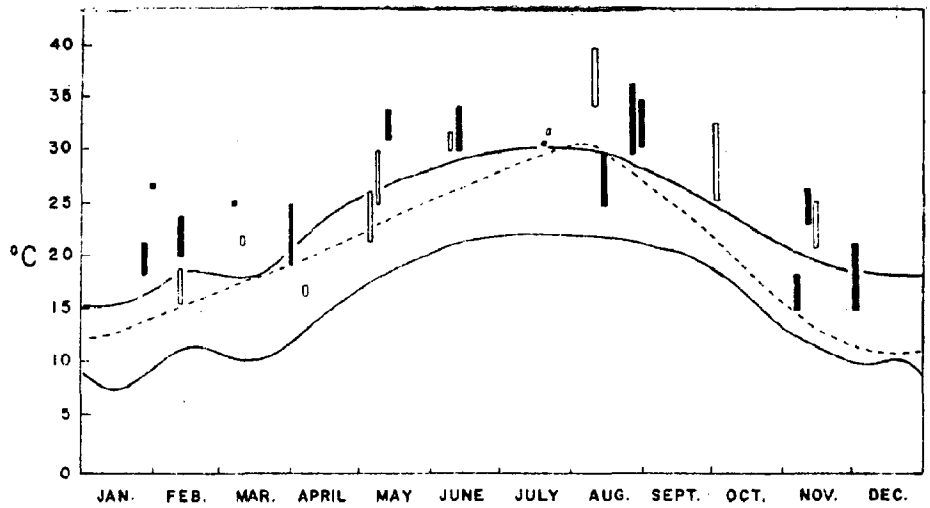
Sapelo Island, Georgia

The salt marshes on the Georgia coast at Sapelo Island are perhaps the most intensively studied marshes in North America. Consequently, these can serve as a case history model for other North American salt marshes.

These marshes occupy wide areas of soft sediment lying between narrow barrier islands and the mainland. The marsh is dominated by the grass Spartina alterniflora which grows in several height forms. The distribution of the marsh and the appearance of the plants is shown in Figure 4 (Teal, 1958a; Teal, 1962). Many studies have been made of the geologic history of these barrier islands (Figures 5 and 6). These show that the present sea islands of the Georgia coast represent islands which formed as the sea retreated during the last period of continental glaciation and which are now being slowly drowned (re-invaded) by a rising ocean (Hoyt et al., 1964; Land and Hoyt, 1966; Hoyt and Hails, 1967; Hoyt and Henry, 1967). Growth of the major plants and animals in these marshes has been studied in great detail. Pomeroy (1959) studied the productivity of algae in these salt marshes, finding that there was a nearly constant daily gross production throughout the year and that this amounted to 200 grams carbon/m^2/yr. Figures 7 and 8 show Pomeroy's study site and some data for gross algal production and respiration. Smalley (1959) determined the net primary production of Spartina alterniflora (the dominant marsh grass) (Figure 9) and Teal and Kanwisher (1961) have summarized all of the feeding relationships occurring among the major plants and animals. Smalley (1959) studied feeding of snails and grasshoppers (Figure 9), and Kuenzler (1961a; 1961b) studied the energy flow and phosphorus metabolism of horse mussel (Modiolus) populations (Figure 11). Using these and other available data, Teal (1962) was able to construct an energy flow diagram for the Sapelo Island marsh system (Figure 12). This is, to date, the only such diagram for a salt marsh system in North America. This diagram provides the necessary basic knowledge to understand energy movement and nutrient cycling through a salt marsh and provides the foundation upon which a rational system of marsh management can be built.

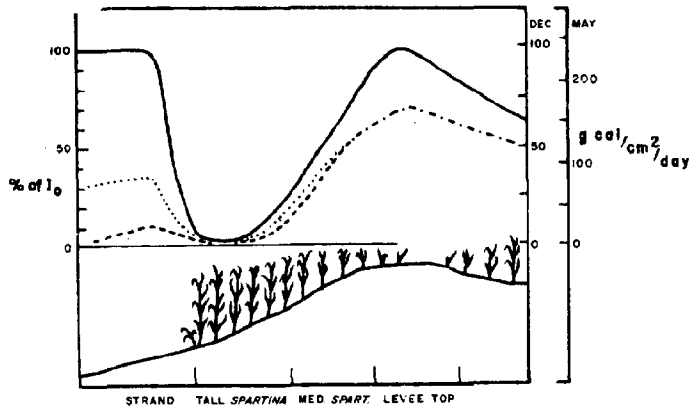
TYPES OF SALT MARSH IN THE UNITED STATES

There are two major groups of salt marshes in the United States--those characteristic of the East and Gulf Coasts on the one hand and those characteristic of the West Coast on the other. This segregation is supported first of all by major differences in physiography. East coast estuaries, and their associated marshes, form on a rather gently sloping coast with a broad continental shelf under conditions of a sea which is slowly rising relative to the land. West coast estuaries, on the other hand, are formed in rather narrow river mouths which drain almost directly onto a steep continental slope. Consequently, estuaries and marshes are more limited in their development on the West Coast.



Seasonal variations in temperature in salt marshes near Sapelo Island, Georgia. *Solid vertical bars:* observed daytime temperature range of surface of bare sediments. *Open vertical bars:* observed daytime temperature range of surface sediments under tall *Spartina*. *Broken line:* water temperature at mouth of Duplin River. *Solid lines:* maximum and minimum air temperature at Sapelo Island (Monthly means for 1956–7. Jan. 1956–April 1957 recorded by author; April–Dec. 1957 from U. S. Weather Bureau 1957.).

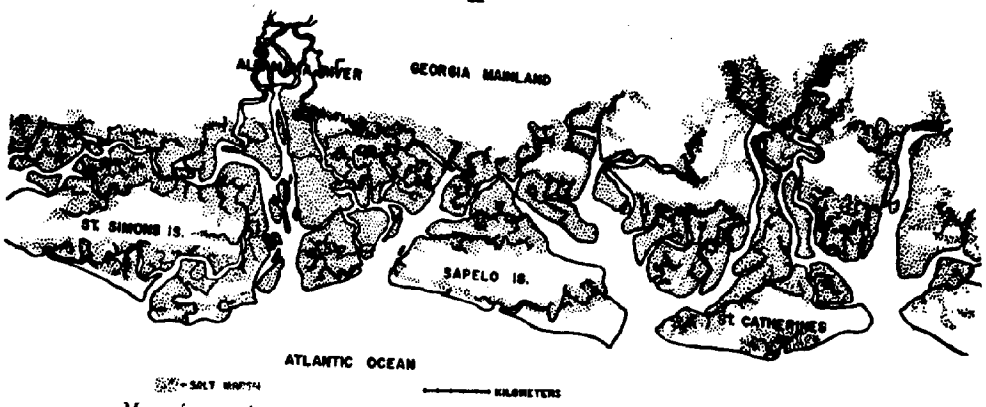
Fig. 3B. Seasonal change in temperatures in a Georgia salt marsh (Pomeroy, 1959)



Per cent of incident light reaching surface of sediments in different zones of marsh of Duplin River as measured with a photometer. *Solid line:* sediments exposed to air and full sun. *Dotted line:* sediments at mean depth of water for the period of flooding. *Dashed line:* sediments at maximum depth at high water. Scales at right give estimated maximum and minimum daily insolation for day of average cloudiness (based on Kimball 1928, Table 4).

Fig. 3C. Percent light reaching surface of sediments in a Georgia salt marsh (Pomeroy, 1959).

A



Map of part of coastal Georgia showing salt marsh area between sea islands and mainland.

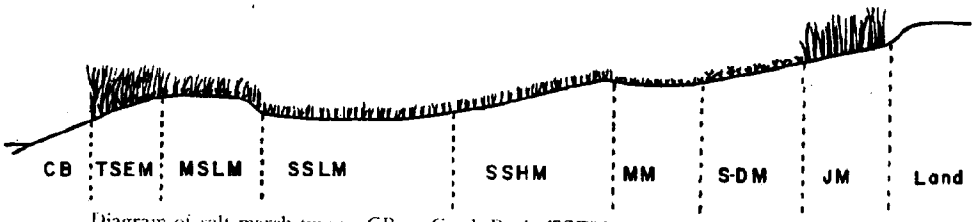
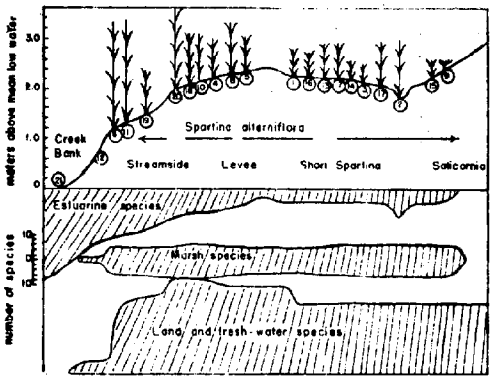


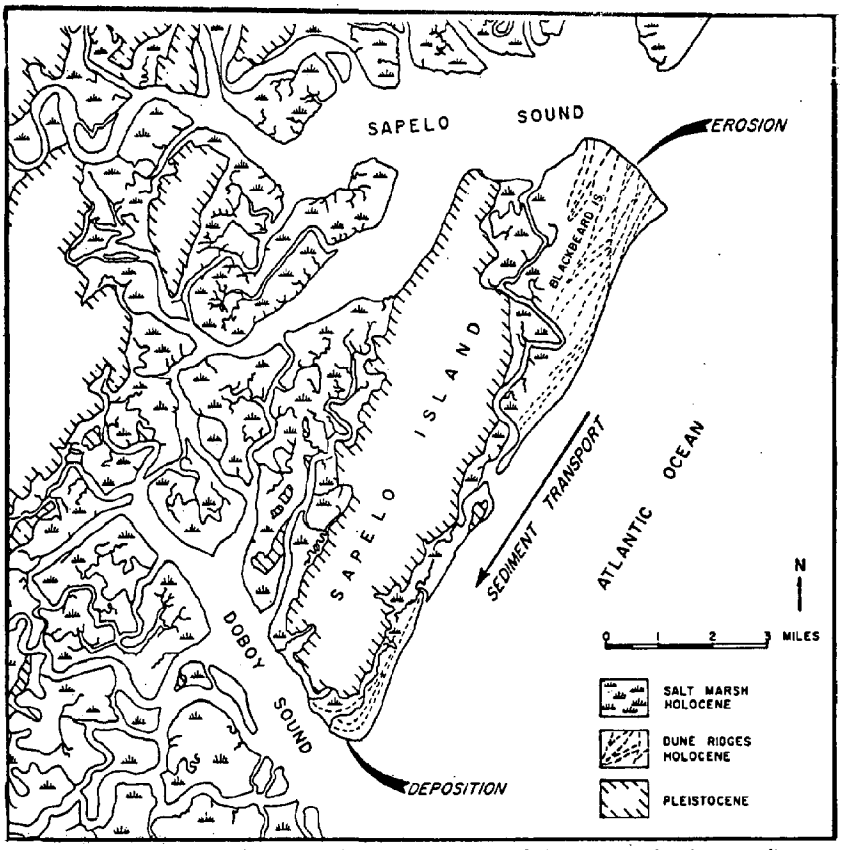
Diagram of salt marsh types. CB = Creek Bank, TSEM = Tall Spartina Edge marsh, MSLM = Medium Spartina Levee marsh, SSLM = Short Spartina low marsh, SSHM = Short Spartina High marsh, MM = Minax marsh, S-DM = Salicornia-Distichlis marsh, JM = Juncus marsh.

B

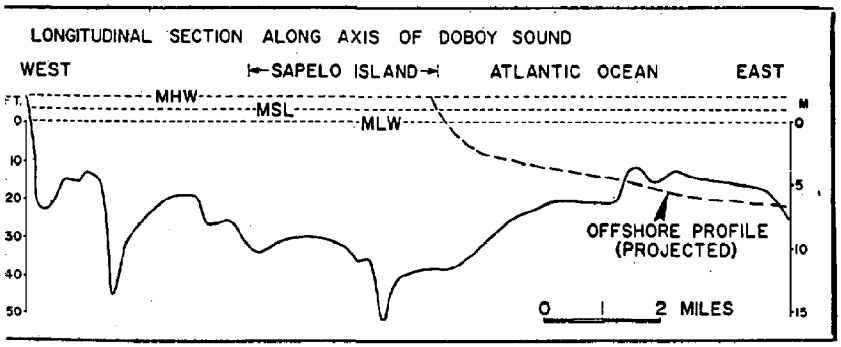


Representative section of a Georgia salt marsh with horizontal scale distorted non-uniformly. Sample sites indicated by circled numbers. Site 2 represents the beginning of a drainage channel, not an isolated low spot. Symbols for grass are drawn to correct height for average maximum growth at those sites. The number of species of animals of 3 groups listed in Table I are plotted against sample sites. Names of marsh types used herein are also indicated.

Fig. 4. Diagrams of zonation of communities in salt marshes near Sapelo Island, Georgia. A from Teal, 1958a and B from Teal, 1962.

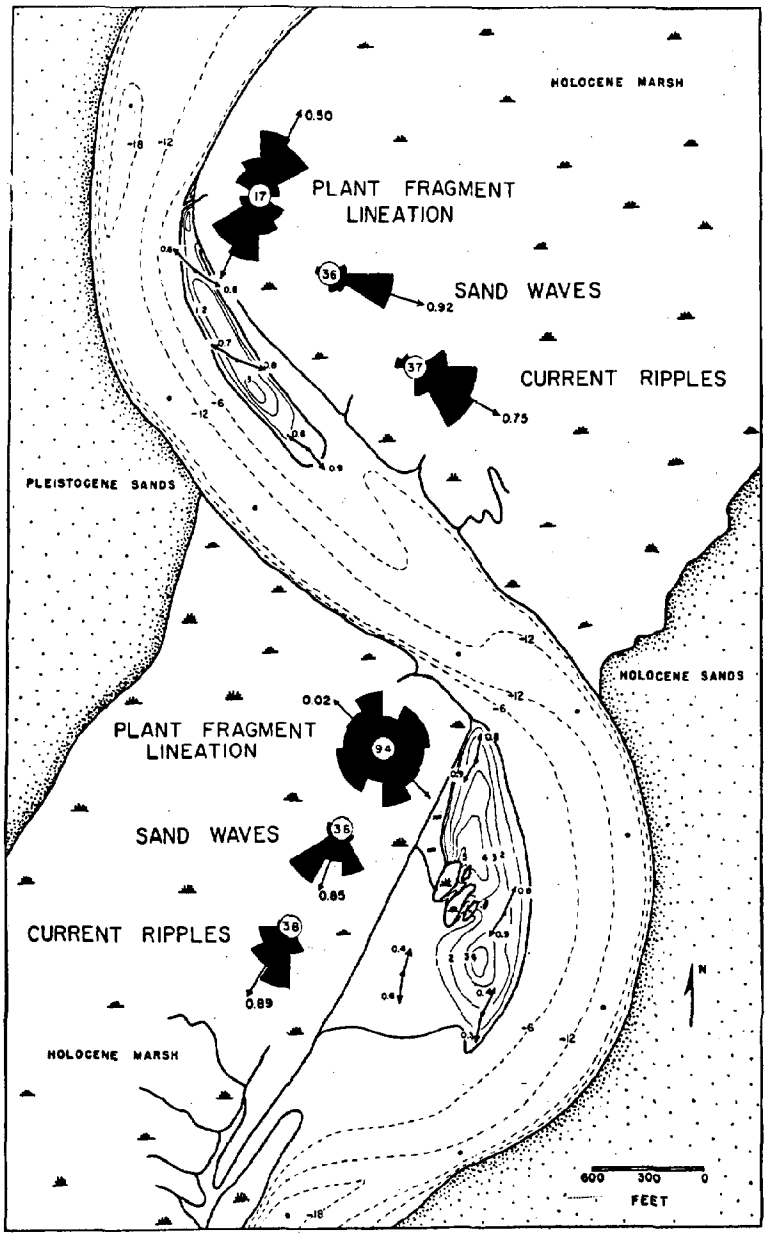


Map of Sapelo Island, Georgia, showing distribution of Pleistocene and Holocene sediments, lune ridges on Blackbeard and Sapelo islands, and dominant longshore drift



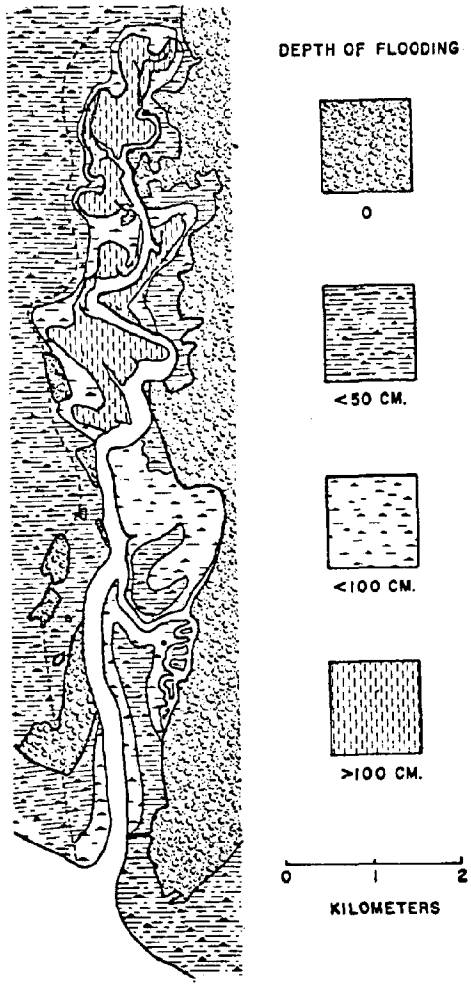
Longitudinal section along maximum depth of Doboy Sound, Georgia; offshore section way from influence of channel (dashed line). Symbols: MHW = mean high water; MLW = mean w water; MSL = mean sea level.

Figure 5. Illustration of present character of Sapelo Island, Georgia showing marshes and barrier islands (from Hoyt and Henry, 1967).



Map showing the relation of Blackbeard Creek to the outcrops of Pleistocene and Holocene sands, the configuration of the two point bars and the estuary channel (contours in feet relative to mean low water), direction and velocity (in knots) of ebb and flood currents flowing over the bars, and orientation roses for directional properties for each bar. Numbers in the center of the orientation roses give the sample size. The consistency ratio is recorded at the head of the vector resultant arrow in each case. Dots in the channel axis are samples relative to Fig.5.

Figure 6. Illustration of factors influencing sedimentation in meandering creeks near Sapelo Island, Georgia (from Land and Hoyt, 1966).

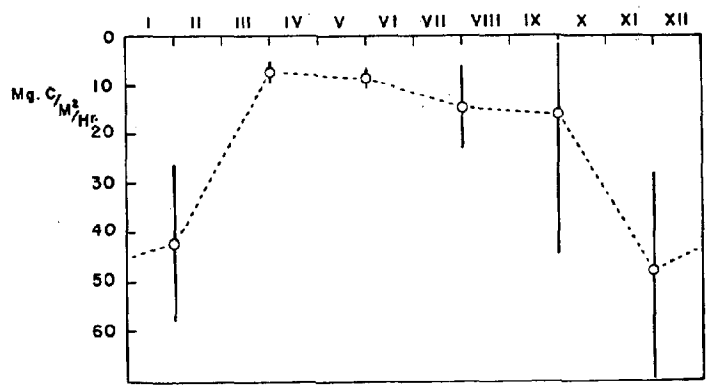


Map of the Duplin River and its intertidal marshes. Contours represent depth of water at spring tide and are at high-water line, 50 cm below high water, 100 cm below high water, and 200 cm below high water (low water line). The 150-cm contour is omitted for clarity. Sapelo Island is on the right. The limit of drainage is shown by the dotted line. Outline of land and water areas from U. S. C. and G. S. Chart 574. Depths are from survey described in text.

Fig. 7. Map of Duplin River study site where research on algal productivity in Georgia salt marshes was carried out (From Pomeroy, 1959).

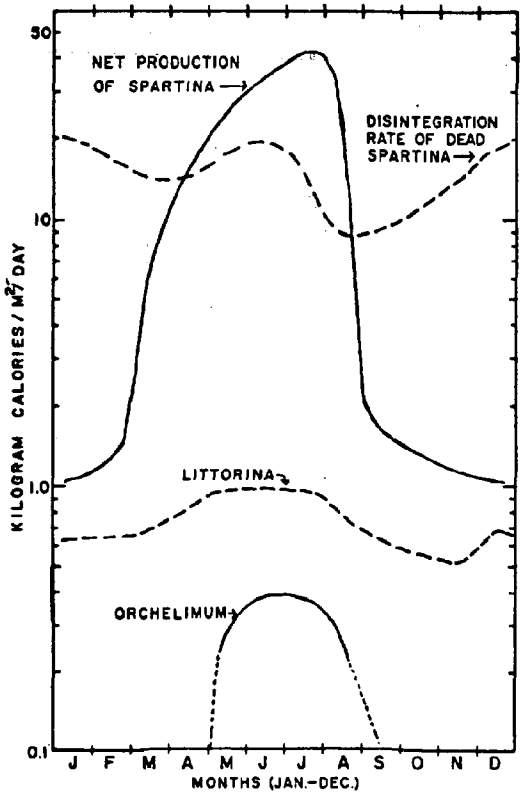
Gross algal production in various zones of the marsh of the Duplin River, mg C/m²/day

Zone		Month					
		1-2	3-4	5-6	7-8	9-10	11-12
Bare strand	In air	+397	+3	+35	+78		+307
	In water	+415	+315	+777	+1541		+528
	Total	+812	+318	+812	+1619		+825
Tall *Spartina*	In air	+72	+12	0	+59	+120	+478
	In water	+275	+210	+518	+1027		+352
	Total	+347	+222	+518	+1086		+830
Medium *Spartina*	In air	−37	+120	+93	+17		+860
	In water	+183	+140	+346	+685		+234
	Total	+146	+260	+439	+702		+1094
Levee top	In air	+495		+52	+29		+228
	In water	+138	+105	+259	+513		+176
	Total	+633		+311	+542		+404



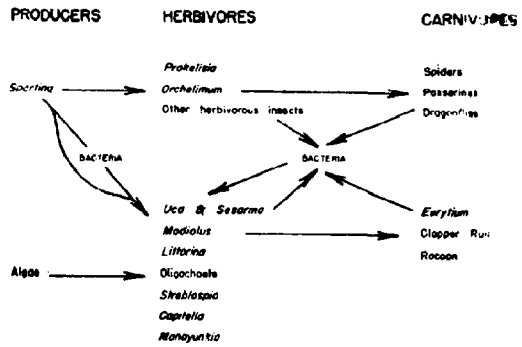
Respiration in air of organisms in marsh sediments at various seasons. Each point is a two-month mean, with vertical bars representing 95 per cent confidence limits.

Fig. 8. Data for gross algal productivity and for respiration in marsh sediments at Sapelo Island, Georgia (From Pomeroy, 1959).



—Comparison of the annual pattern of energy flow in *Littorina* and *Orchelimum* populations in relation to certain potential food sources. Net production of *Spartina* in the low marsh is the sole source of food energy for *Orchelimum* while the disintegration of dead *Spartina* through the entire marsh and the subsequent transport of detritus (including associated microflora) to the high marsh provides one potential food source for *Littorina*.

Figure 9. Comparison of annual patterns of productivity in salt marsh grass (Spartina alterniflora) and in two salt marsh animals (Littorina--a snail, and Orchelimum--a grasshopper) at Sapelo Island, Georgia (from Odum and Smalley, 1959).



Food web of a Georgia salt marsh with groups listed in their approximate order of importance.

Fig. 10. Food web of a Georgia salt marsh (from Teal, 1962).

A

Flux rates of energy in a Modiolus *population, in kg-cal/m²/yr*

Growth:	Body	3.7	
	Shell	8.4	
	Byssus	1.8	
Reproduction (gametes):		2.8	
TOTAL PRODUCTION			16.7
Respiration:	Water	11	
	Air	28	
TOTAL RESPIRATION			39
ASSIMILATION			56

B

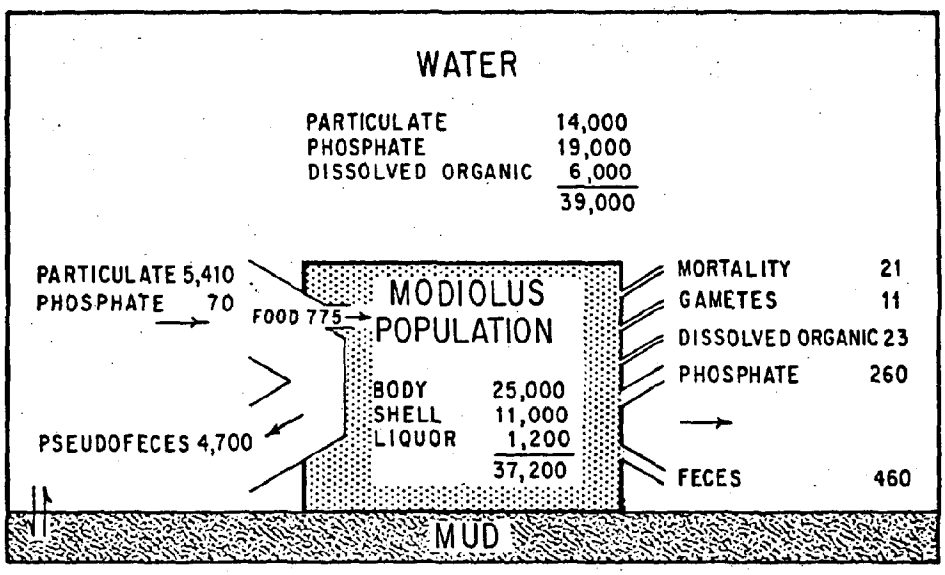
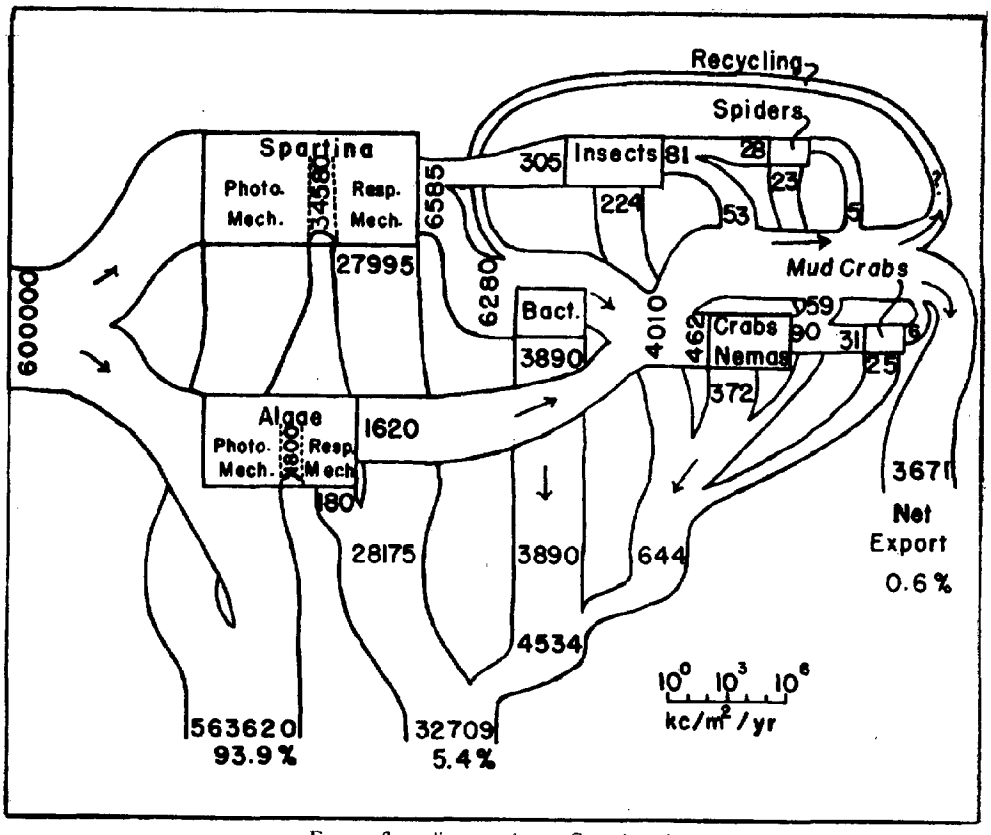


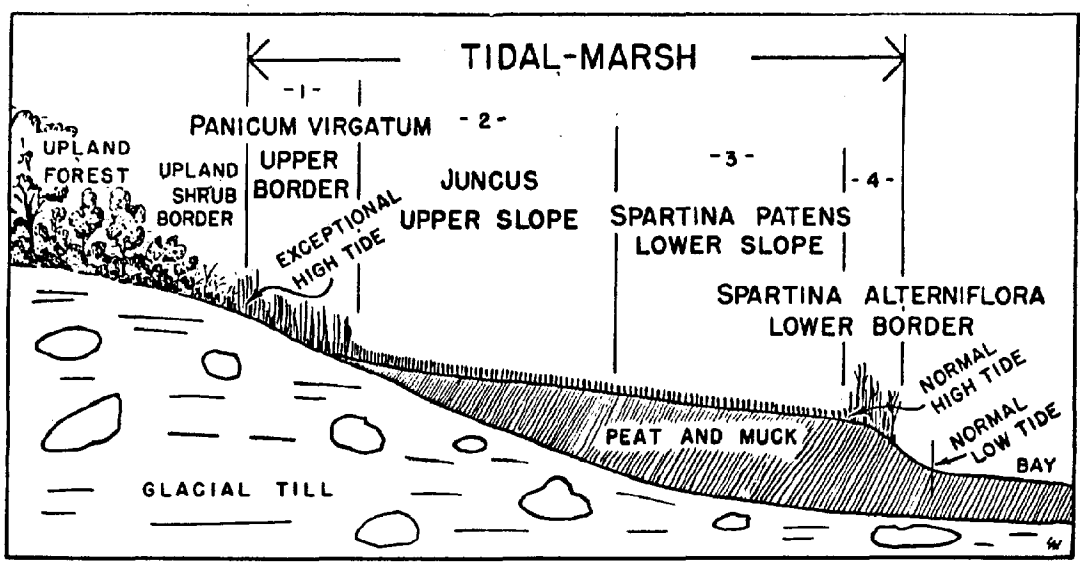
Diagram of phosphorus flow through the mussel population. Values for the water and the mussel population are μg P/m²; rates are μg P/m² day. The flux rates of phosphorus in food and pseudofeces are calculated values necessary to balance the other, measured flux rates.

Figure 11. Flux rates of energy movement (A) and phosphorus flow (B) in a horse mussel (Modiolus) population in Sapelo Island, Georgia, salt marshes (A from Kuenzler, 1961a and B from Kuenzler, 1961b).



Energy-flow diagram for a Georgia salt marsh.

Fig. 12 Energy flow diagram for a Georgia salt marsh. Note two major flows, one through the grazers (insects) and the other, larger, through decomposers. Note also large net export from the system (from Teal, 1962).



Diagrammatic cross-section of the upland-to-bay sequence, showing the characteristics of the major vegetational units. Vertical scale much exaggerated.

Fig. 13 Cross-sectional diagram of New England-type salt marsh (from Miller and Egler, 1950).

East Coast Salt Marsh Systems

The salt marshes of the East coast are of three general types. Although many of the dominant plants occur along the entire coast, habitat factors combine in such a way that three clear geographic regions may be recognized (Chapman, 1960). In the Bay of Fundy and on the nearby Canadian coast great tidal ranges act on relatively soft rocks to produce large quantities of reddish silt. These become compacted after deposition providing a firm, primarily mineral, substrate. There are no examples of this type of marsh in the United States. Southward, from New England to New Jersey, where the shore is composed of larger quantities of hard rock, there is much less silt and the marsh substratum is primarily a fibrous marine peat. Along the fringe of the Atlantic Coastal Plain south of New Jersey and into the Gulf of Mexico, large quantities of silt are eroded from relatively soft rocks. Here, long rivers empty into broad estuaries or sounds and the marshes formed are wide, relatively flat, and have a substratum of soft, grey silt.

As indicated, many of the dominant plants occur from Nova Scotia to Texas. The grass Spartina alterniflora is the primary intertidal species, generally occurring from about mean sea level to about mean high tide. Two species of Juncus, J. gerardi and J. roemerianus, are major species at or above the high tide line. J. gerardi occurs chiefly north and J. roemerianus south of Chesapeake Bay. Spartina patens, Distichlis spicata and several species of Salicornia occur just above the mean high water mark throughout the entire Eastern and Gulf coasts. Numerous other species occupy similar wide latitudinal ranges throughout east coast salt marshes.

In the New England type salt marsh (Figures 13, 14 and 15) there appears a rather clear-cut zonation pattern (Miller and Egler, 1950; Nichols, 1920; Niering, 1961; Chapman, 1940a; Redfield, 1965b). Spartina alterniflora occurs in pure stands in the intertidal zone in a belt of varying width. It may merely fringe the creeks in a rather rank growth and thus compose only a small part of the total area of the marsh or, where slopes are more gentle, it may cover a very large area. The substratum is peaty or semi-peaty composed of silt and plant remains. Above the Spartina alterniflora there is always a well-developed zone dominated by Spartina patens mixed with Distichlis spicata. Distichlis is rarely dominant except in the wetter, more poorly drained situations. Dwarf stems of Spartina alterniflora may also be found in this zone. The substratum here is firm and peaty, being made up almost entirely of plant remains. Juncus gerardi forms pure stands in the higher parts of the zone above normal high tides, often forming a fringe at the edges of uplands. Bare areas, or pannes, frequently are scattered throughout the upper portion of the marsh. These may have small plants of Distichlis, Spartina alterniflora, or Salicornia. Around the very fringe of the marsh at the edge of upland there is often a narrow belt dominated by Panicum virgatum and Spartina pectinata with a very great number of other species associated.

Blum (1968) studied the formation of the dense mats of living and partially-decayed stems characteristic of the Spartina patens zone. He found that this mesh of stems formed due to interaction between environmental factors (tide, wind) and growth form features of Spartina patens.

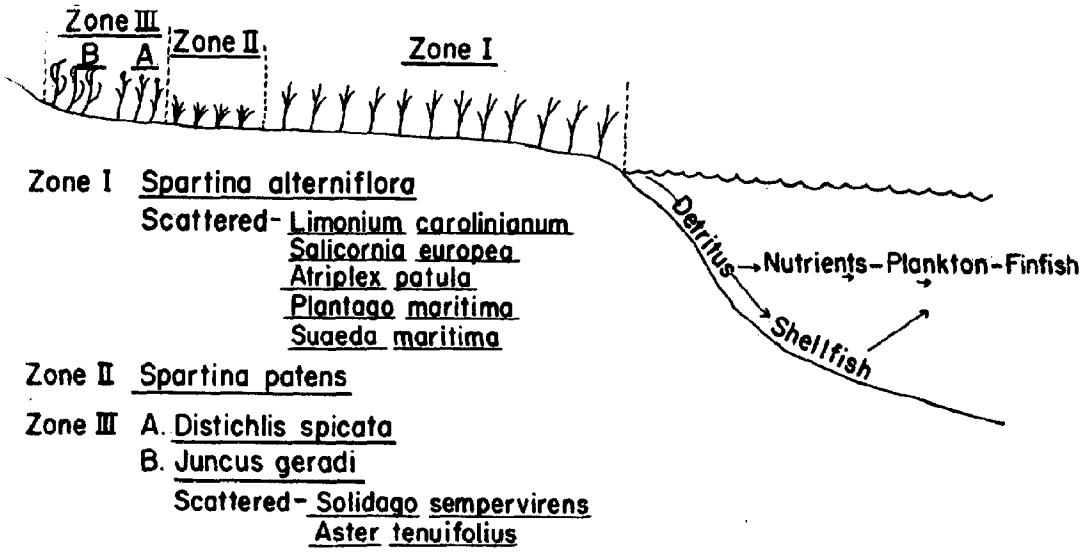
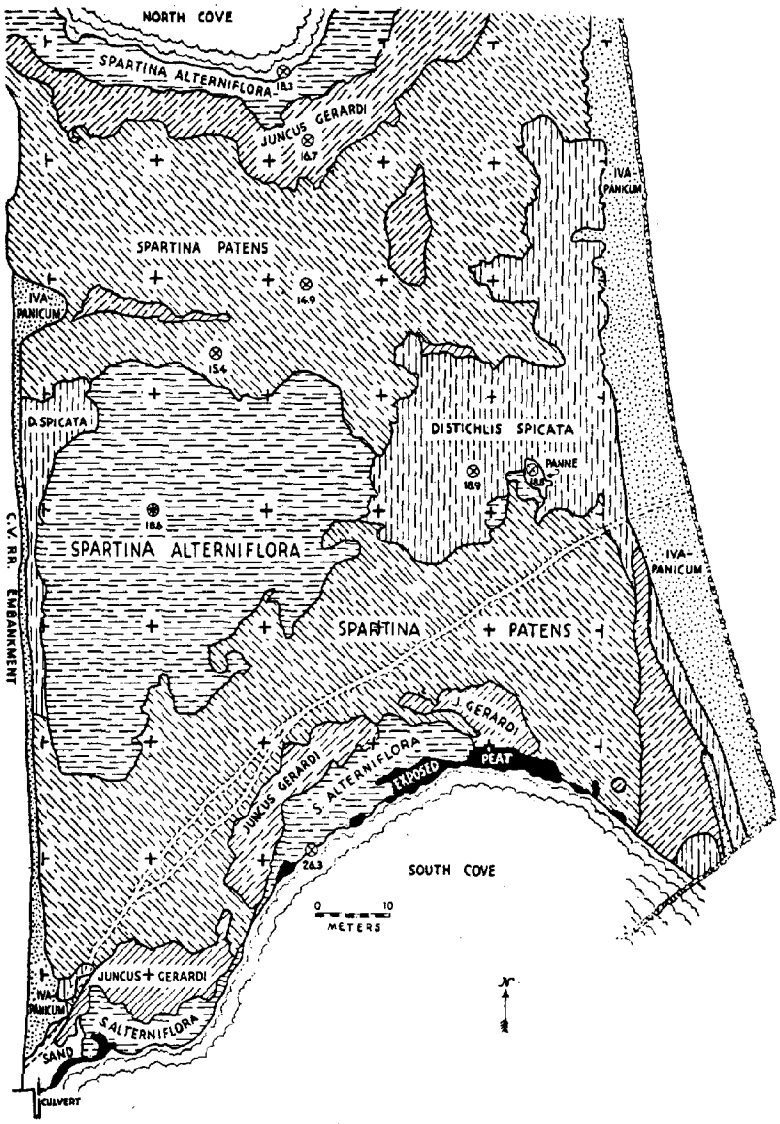


Figure 14. Cross sectional diagram of new England type salt marsh on the North River, Massachusetts (from Fiske, Watson, and Coates, 1966).

Distichlis spicata mats seemed to form in a similar manner. Algal growth was limited under the dense mats, due to low light intensity, whereas in the Spartina alterniflora zone there was an almost ubiquitous algal layer. Blum speculates that the dense mat may conserve detritus within the Spartina patens zone and also serve as a trap for allochthonous nutrients.

On Long Island, a pattern similar to that of New England is found. Long Island salt marshes have been much modified by man. In their original state (Conard, 1924; Conard and Galligar, 1929; Taylor, 1938) Spartina alterniflora typically occupied a small fraction of the marsh area, occurring along the fringes of the marsh, in areas flooded regularly by tides, or on marsh islands. Spartina patens meadows covered the majority of the marsh with fringes of Juncus gerardi and Distichlis spicata on the inner edge of the marsh where it contacted upland. The zones in which Spartina alterniflora was not found were never flooded by the tide except under extreme above-normal conditions.

Farther southward, in New Jersey and Delaware, there is a subtle change from the New England type of marsh to that more characteristic of the South Atlantic and Gulf Coastal Plain. Again, there are relatively limited areas of Spartina alterniflora with the greatest area of the marsh composed of Spartina patens (Fender, 1938; Harshberger, 1909; Martin, 1959; Snow, 1902). Localized areas of high salinity have patches dominated by Salicornia spp. Creeks draining into Delaware Bay show a similar pattern (Good, 1965; Morgan, 1961). Along these creeks there is a tendency for Spartina alterniflora to show a taller growth form along creeks, a pattern very characteristic of marshes farther south. Spartina cynosuroides and Scirpus robustus, both southern species, occur along creeks in Delaware Bay



Map showing zonation of the vegetation on the Mamacoke marsh. The position of the corners of the permanent 15 x 15 m. quadrats are indicated. Points at which salinity measurements were taken are shown by circles, and low-tide salinity values are given in number of grams of salts per 1,000 grams of sea-water.

Figure 15. Map of distribution of major community types in New England type salt marsh near New London, Connecticut (from Niering, 1961).

(Chamberlain, 1951). On the eastern shore of Maryland (Shreve, 1910) the same zonation of Spartina alterniflora grading into Spartina patens with some Juncus gerardi and other species at the marsh border is found. Along the western shore of Chesapeake Bay (Shreve, 1910), there is a stronger influence of fresh water. Here, Spartina alterniflora occurs in areas covered by tides but Spartina cynosuroides often borders tidal streams

near their mouths and replaces Spartina alterniflora up stream from the creek mouth. Distichlis spicata is more abundant than Spartina patens at higher elevations. Species characteristic of fresh water, such as Scirpus olneyi, S. robustus, and Typha spp. are common in the areas with very low salinity. Juncus roemerianus occurs near the mouth of the Potomac (and at Ocean City) in small quantities, increasing in importance toward the mouth of the Bay.

South Atlantic and Gulf Coast Marshes

South of Chesapeake Bay salt marshes typical of those along the entire South Atlantic and Gulf Coasts occur. These represent, in general, the best development of salt marshes in the United States, and consequently will be described in detail. In the southeastern states, salt marshes are formed primarily in estuaries where major rivers, draining large expanses of upland, deposit heavy silt burdens (Linton, 1968). They also form behind barrier beaches (as along the North Carolina coast north of Cape Lookout), and up bays and tributary rivers as far as there is an influence of salt water. At their southern limits, they grade into mangrove forest in south Florida. Similar marshes also occur along the Gulf Coast into Texas. Although there is an overall similarity in the marshes of this area, several distinct regions can be recognized.

Behind the Outer Banks of North Carolina south to Cape Lookout, fringing the inner shores of North Carolina's vast brackish sounds and in the Virginia Beach, Virginia area, irregularly flooded marshes occur. Here tidal amplitudes are very limited and there often are rather great changes in salinity of the ground and flooding water. In these marshes, the tidal amplitudes are usually less than a foot and higher tides are wind-driven and associated with storms and rapid changes of wind direction and velocity accompanying the movement of fronts into the region. In these marshes, Spartina alterniflora seldom occurs in extensive stands and generally is found fringing the edge of rather straight tidal creeks. The substratum is generally hard sand and peat.

There are two major community types in these marshes (Waits, 1967). Black needlerush occurs in vast, pure stands lying at an elevation just above mean high water. There are almost 100,000 acres of this type of marsh in the counties fringing Pamlico Sound, North Carolina, and the vast majority of this is Juncus roemerianus marsh. Few other species occur in this marsh type. On slightly higher ground, along the edge of creeks or at the heads of creeks where sand may accumulate, Baccharis halimifolia, Borrichia frutescens, and Spartina cynosuroides may occur. The other community type is dominated by Spartina patens, and resembles the salt meadows of New England marshes. Here, Spartina patens forms extensive stands overlying several inches of raw, brownish peat. Distichlis spicata, Scirpus robustus, and Pluchea purpurascens are scattered throughout, but these rarely become dominant. Locally, wet openings and ponds occur in these meadows. These form favorite feeding sites for overwintering waterfowl and, during the summer, for wading and shore birds.

Variations in habitat factors in these marshes are less clearly associated with community types than in some other salt marshes (Waits, 1967). Although there is little apparent difference in elevation, the species maintain the same general elevational relationships found in the low marsh. Spartina alterniflora is confined to the intertidal creek banks with Juncus roemerianus

occurring slightly higher just above mean high water. Spartina patens, in general, is slightly higher than Juncus roemerianus. The ponds, occurring in the Spartina patens zone, often are just enough lower than the surrounding vegetation to permit water to accumulate. Usually the standing water is fresh to brackish. Occasionally, salt water may penetrate into a pond. When it does, stands of Spartina alterniflora and Salicornia sp. develop, with much initial establishment of Spartina alterniflora from seed. The consequent vegetation is greatly different from that of the brackish ponds. The substratum appears to be a uniform, unsorted sand and the elevational differences in the surface communities reflect elevational differences in the original surface of the sand. With the exception of the salt ponds, where salinities often greatly exceed sea strength, the highest salinities are in the Juncus roemerianus zone. Salinity is considerably less in the Spartina patens areas. Standing water is present in the Juncus roemerianus areas only as a result of wind-driven tides. Drainage is otherwise good. In Spartina patens, on the other hand, rainwater may accumulate at any time, but particularly in late fall-winter and in mid-summer. This zone often goes completely dry in early summer or autumn.

From Cape Lookout, North Carolina, south to the Jacksonville, Florida, area the optimum development of salt marsh in the United States is found (Linton, 1968). These marshes, often called low marshes, form behind narrow barrier islands in areas influenced by heavy silt deposition from large rivers. There is a relatively small amount of open water behind the barrier islands (Figure 4). Tidal amplitudes are variable, ranging from two to five feet in North Carolina and northern Florida, to as much as eight feet in Georgia and South Carolina. Although marshes throughout this entire region are similar, those from Cape Lookout to Myrtle Beach, South Carolina, are somewhat less extensive and well-developed than those from Myrtle Beach to Jacksonville. This latter area includes the famous Sea Islands of South Carolina and Georgia.

The characteristic feature of these marshes is the vast expanse of Smooth cordgrass Spartina alterniflora which covers the soft, grey sediments between mean sea level and approximately mean high water. These broad, nearly level expanses of grass and soft sediment develop, under the influence of high tidal amplitudes, dendritic creeks and deep tidal channels in vast number, giving the marshes a characteristic dissection pattern when viewed from the air. The slow, gentle subsidence of these South Atlantic marshes also contributes to formation of these intricate creek patterns.

Several distinct community types (Figure 4) may be recognized within the South Atlantic salt marshes (Reed, 1947; Kurz and Wagner, 1957; Teal, 1958a, 1962; Adams, 1963). Although these are reasonably well-defined and characterized by a clear combination of physiographic and biotic features they actually grade into one another so that the marsh is in reality a series of communities which change gradually from the tidal creeks to higher ground.

Along the creek banks, below the level of vascular plants, there is a zone which is usually exposed on every low tide. Here the substrate is usually very soft, being composed primarily of grey silt. Occasionally sandy areas occur. These bare sediments are covered with blooms of benthic algae, primarily diatoms, at various times of the year. Along the banks of the creeks, from approximately mean sea level to the crest of the levee (the raised portion

found along the bank of most creeks) Spartina alterniflora reaches its tallest growth, averaging from four to eight or even ten feet in height. Because of the great size of the culms, density of plants here is generally lower than in the other marsh communities. The substratum is very soft and silty and one may sink as deep as his waist when walking across this community. On the top of the natural levee along the creek a zone of Spartina alterniflora of medium (two to four feet) height occurs. The substratum, although still soft, is more firm than on the creek bank. Away from the streams the Spartina alterniflora decreases to less than a foot in height in the Short Spartina alterniflora marsh. Here the surface is very nearly level and the substratum much firmer than in the other zones due either to a dense network of roots and rhizomes or to high sand content. In the higher, sandier parts of the community, near the mean high water mark, the Short Spartina alterniflora is mixed with Salicornia spp. and Limonium spp. Frequently, open sandy areas entirely devoid of vegetation, or with scattered stands of Salicornia and Distichlis spicata occur in this zone. At slightly higher elevations there is a community dominated solely by Juncus roemerianus. This often occurs in isolated patches throughout the Spartina alterniflora zone, primarily in the areas of shortest growth. At the edge of uplands where there presumably is some rather regular seepage of fresh water, extensive stands of Juncus roemerianus are found.

Few data are available on the general proportions of the different communities in a given area of marsh. At Sapelo Island, Georgia (Teal, 1962), 20 % of the marsh was creek-bank and Tall Spartina alterniflora. 35 % Medium Spartina, and 45 % Short Spartina and Salicornia. In Brunswick County, North Carolina, our measurements show that 6 % of the area was Tall Spartina alterniflora, 11 % Medium, and 47 % Short. Juncus roemerianus occupied 9 % of the area and creeks 27 % No estimate of creek banks was made. Despite the differences in methods and communities recognized, these data do demonstrate that any given large area of marsh is almost half Short Spartina alterniflora and that the creek bank and Tall Spartina alterniflora zone is less than 20 % of the total area. Further, they suggest that farther northward the proportion of Short Spartina alterniflora increases relative to the other Spartina community types.

The major variations in habitat in these marshes stem from differences in elevation, and their consequent effects on duration of tidal inundation, and from substrate differences. The Tall Spartina alterniflora zone is deeply and regularly flooded by salt water and the Short Spartina alterniflora - Salicornia - Limonium zone is flooded less regularly and less deeply. The higher portions of the marsh are flooded only on spring and storm tides. Although there is much variation in salinity, it appears that concentrations approximately equal to sea strength are found in the Tall and Medium Spartina alterniflora along the creeks. Furthermore, salinity increases with distance from the creeks, reaching its highest values near mean spring high tide in the sandy Short Spartina alterniflora zone and in the bare sand flats. Values in excess of twice sea strength can regularly be recorded on the sand flats and it appears that continued exposure to salinities this high prevents vascular plants from growing. There are relatively few data, other than those for salinity, regarding variations in the chemical composition of the substratum. Sulfides are present in large quantities in the soft, silty materials and when these are oxidized sulfuric acid is produced. Thus, although the pH of the fresh silt may be circum-neutral, upon drying it may drop as much as 3 whole pH units. It has been suggested that local drying and consequent

increase in acidity may account for localized areas of plant die-out in marshes. No variations in ionic composition of the soil water (other than salinity) have been clearly implicated in plant distribution. In a North Carolina marsh Adams (1963) found that soluble iron concentrations were higher in the lower portion of the marsh. In nutrient culture experiments, he found that Spartina alterniflora became increasingly chlorotic with either decrease in iron or sodium chloride, leading him to suggest that iron concentrations may, in part, limit growth of Spartina alterniflora in the higher portions of the marsh.

Above mean spring high tide out of the area dominated by Spartina alterniflora and Juncus roemerianus, Spartina patens abruptly becomes the dominant. Distichlis spicata, Borrichia frutescens, and Solidago sempervirens are the other major plants of this zone, often referred to as "High Marsh." Here the soil is usually very sandy and the salinity is much lower than that of the low marsh. Scattered shrubs, such as Baccharis halimifolia and Iva frutescens usually occur in this zone, which often gives way abruptly to a shrub thicket.

As one progresses away from immediate sources of salty ocean water up rivers and their tributary streams, gradual but clearly defined changes in marsh composition take place. Along creeks and rivers of moderate size Spartina alterniflora becomes progressively less abundant and more confined to areas immediately along the water's edge. Juncus roemerianus gradually occupies a greater proportion of the marsh and there often are large patches of Distichlis spicata near the inland margin of river marshes. Farther upstream, where waters are predominantly fresh and saline tides penetrate only under extreme conditions, the true salt marsh species give way to species of brackish or fresh water, first Cladium jamaicense and then Typha spp. Numerous herbaceous species with showy flowers, such as Hibiscus moscheutos and Kosteletzkya virginica occur in this zone. These herbaceous marshes in turn give way, usually rapidly, to fresh water Gum-Cypress swamps or to Pocosins. As one might expect, all possible degrees of variation are found and in many cases the salt marsh species may extend for great distances up rivers away from the ocean.

Recently, several studies have been made of the effect of environmental factors on seed germination and seedling growth of several southeastern marsh species. Juncus roemerianus (Seibert, 1969) seed can germinate as soon as they are shed and require light and constant wetness to do so. Germination is best in 0% salinity and occurs up to 1% salinity. Seed exposed to salinities of 2-3% for a short time (21 days) show over 75% germination when placed in distilled water whereas few seed treated similarly for 72 days germinate. Thus, prolonged exposure to salinities over 1% seem detrimental to the seeds.

Mooring (1970) studied germination in seeds from the three height forms of Spartina alterniflora in North Carolina. Although seed were capable of germination when shed, they do not do so in nature. As the seed are continually subjected to tidal flooding a requirement for moist storage is not surprising. Less than 1% of seeds stored dry at 72°F for 40 days were viable. Although seeds stored dry at 43°F germinated after 40 days, none germinated after 8 months. Seed stored 8 months in sea water at 43°F showed 52% germination. Germination over 50% was obtained only in alternating thermoperiod (65-95) and not in constant 72° temperatures. Seed germinated best in fresh water and germination was inhibited at higher salinities due to an osmotic effect. There was no difference in performance of seeds from the three height forms in any germination experiment.

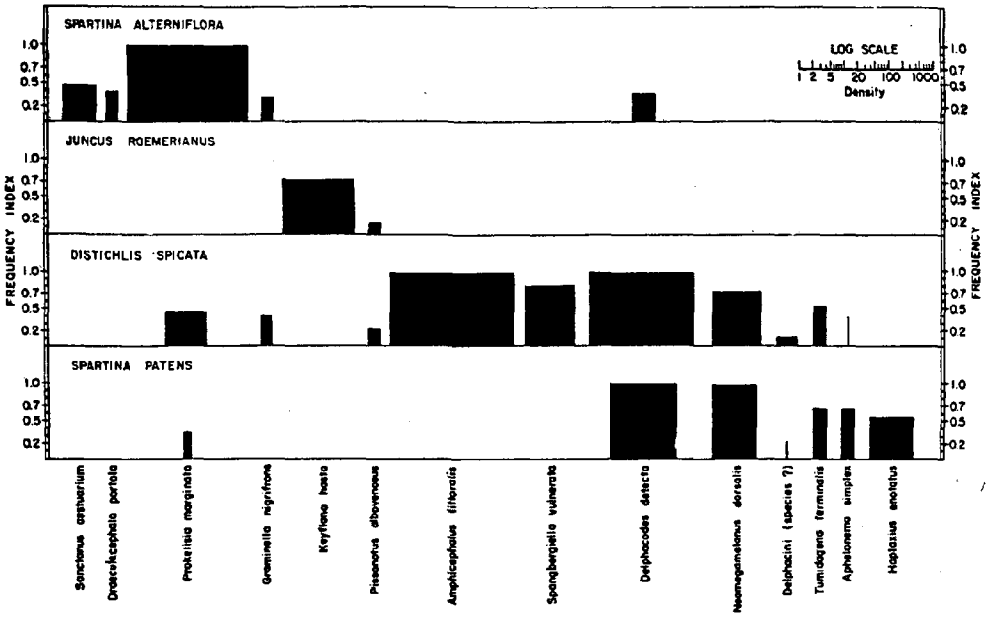
With respect to salinity, seedling growth requirements in Spartina alterniflora differed from those for seed germination. Seedling growth response did not decline gradually as salinity increased. Seedlings grown in 0.5% NaCl weighed more than those grown in 0% or 1.0% NaCl, and grew taller in both 0.5% and 1.0% NaCl than in 0% NaCl. Only at 4.0% NaCl was growth clearly lower than in the controls (0% NaCl). Mooring found that all seedlings exhibited iron chlorosis which was relieved by foliar applications of ferrous sulfate. Adams (1963) reported similar chlorosis in mature plants in nutrient culture. No differences in seedling growth due to height form of the parent plant could be detected. Mooring's work supports the contention that height forms are ecophenes.

In Spartina patens (Seneca, 1969) seed germination also was greater under alternating thermoperiods (65-85 and 65-95) and there did not appear to be cold treatment requirement. Germination response to salinity was found to be curvilinear, being only slightly lower at 2% NaCl than at 0% NaCl. The upper salinity level for germination appeared to be 4% NaCl.

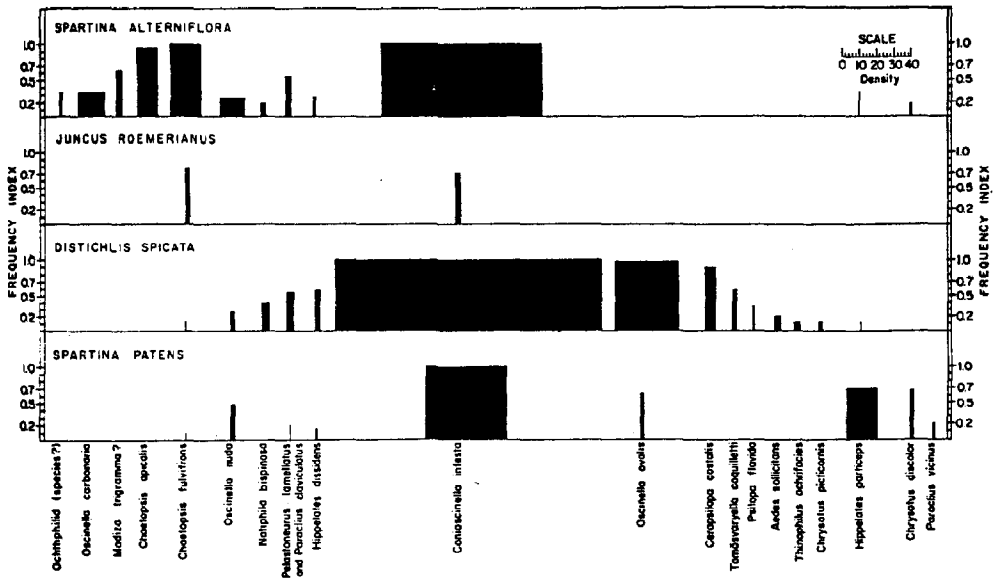
Amen et al. (1970) studied another high marsh species, Distichlis spicata. This species sets dormant seeds which have a low temperature after-ripening requirement. Stratification, lateral scarification and nitrate ion are effective agents in breaking dormancy and stimulating seed germination. Germination was not promoted by saline water, even in a dilution of 1:10. When seeds were stored at 4°C for 1, 2, 3, or 4 weeks, those stored longest showed the highest germination in distilled water. There was also a 14 day periodicity of high and low germination, suggesting possible coincidence with 14 day cycles of neap and spring tides. Amen et al. suggest that dormancy is due to an endogenous inhibitor which accumulates late in maturation blocking nitrate reductase activity in the endosperm. During low temperature after-ripening either decay of the inhibitor or uptake of nitrate induces reductase activity thus overcoming the inhibitor.

Based on these data, certain generalizations can be made about the interplay between seed and seedling physiology and environmental factors. Inasmuch as seed germination in most species is best in fresh water it is reasonable to conclude that it probably occurs in nature when high rains occur during periods of low tide. Spartina patens, a species normally found in the high marsh where tides penetrate irregularly, has a wider range of salt tolerance for high germination than other species. Spartina alterniflora, on the other hand, shows successful germination over a greater salinity range than Spartina patens, although it shows a gradual decline in germination response in relation to increasing salinity. These differences agree with the average and extreme salinity conditions expected in the elevational ranges normally occupied by these species.

Although the common larger animals of these marshes are well known, the distribution and populations of lesser animals, particularly invertebrates, are much more poorly understood. The most thorough study is that of Teal (1962) which summarizes work done by a number of investigators on Sapelo Island, Georgia. Davis and Gray (1966) give data for insect populations in marshes in the vicinity of Beaufort, North Carolina (Figure 16). The Salt marsh grasshopper (Orchelimum fidicinium) and the Salt marsh plant hopper (Prokelisia marginata) are the two major herbivores, Orchelimum eating Smooth cordgrass tissues and Prokelisia sucking the juices. These and other less numerous insects support spiders, wrens, and sparrows. Relatively speaking, a low proportion of the total energy flow of

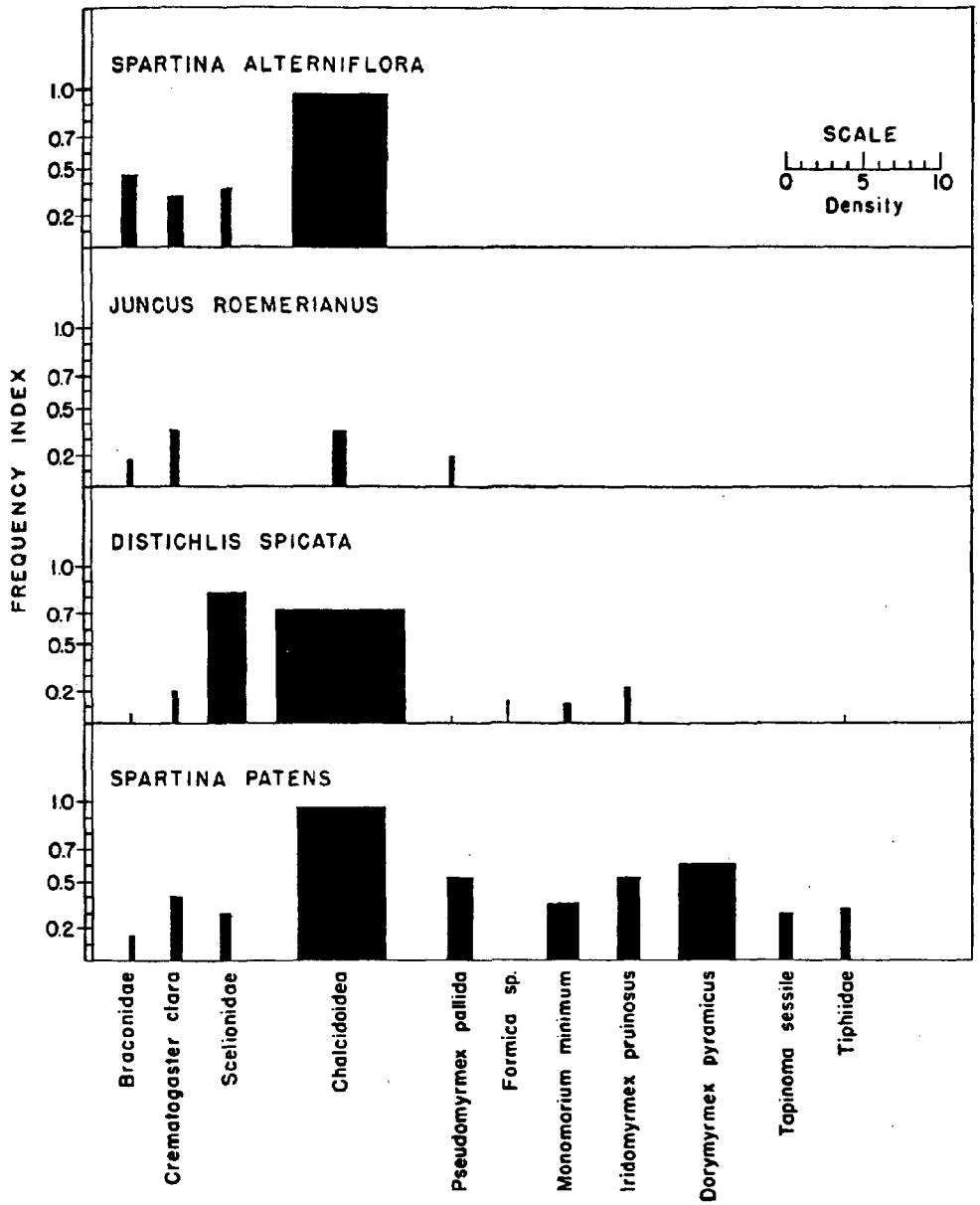


Frequency-density diagram of the principal species of Homoptera from the herbaceous strata of four zones of salt marsh vegetation, based on samples taken during the summer of 1960.



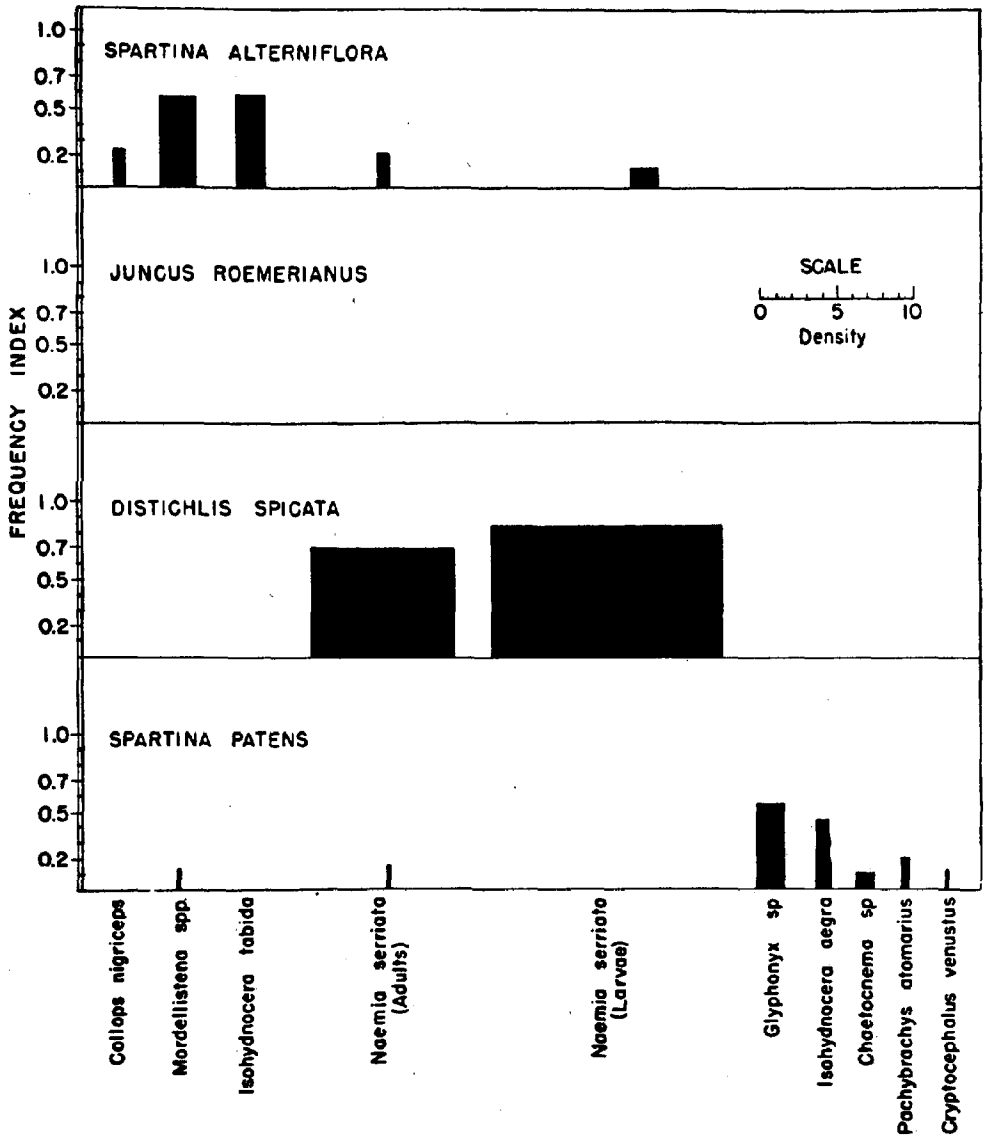
Frequency-density diagram of the principal species of Diptera from the herbaceous strata of four zones of salt marsh vegetation, based on samples taken during the summer of 1960.

Fig. 16A. Insect distributions in salt marsh (Davis and Gray, 1966).



Frequency-density diagram of the principal species of Hymenoptera from the herbaceous strata of four zones of salt marsh vegetation, based on samples taken during the summer of 1960.

Fig. 16B. Principal insect species in salt marshes near Beaufort, N.C. (Davis and Gray, 1966).



Frequency-density diagram of the principal species of Coleoptera from the herbaceous strata of four zones of salt marsh vegetation, based on samples taken during the summer of 1960.

Fig. 16C. Insects in salt marshes near Beaufort, N.C. (Davis and Gray, 1966).

the marsh moves through the grazing, herbivore-based food chain. A much larger group of organisms lives at or near the mud surface feeding on organic detritus, formed by bacterial decomposition of Spartina alterniflora and on algae. Spartina alterniflora stems are broken down by bacteria. These reduce the total amount of organic matter present but increase its food value (de la Cruz, 1965). The most conspicuous algae-detritus feeders are Fiddler crabs (genera Uca and Sesarma), Horse mussels (Modiolus demissus), and the Salt marsh periwinkle (Littorina irrorata), in addition to a variety of annelid worms, oligochaetes, and insect larvae. These, in turn, may be eaten by Mud crabs (Eurytium limosum), Clapper rails (Rallus longirostris), Raccoons (Procyon lotor). These relations hold for the Smooth cordgrass-dominated areas. Little is known of the animal populations and feeding relationships in the Juncus roemerianus marsh, except that insect populations are much more meager than in Spartina alterniflora (Davis and Gray, 1966).

In addition to the animals of the marsh proper, a great variety of immature and mature fish and shellfish are found in the tidal creeks and shallow waters associated with the marsh. Mature oysters (Crassostrea virginica, Hard clams (Mercenaria mercenaria), Blue Crabs, larval and mature shrimp of several species, and the juvenile and mature forms of many fish such as flounder, bluefish, menhaden, croaker, and tarpon are commonly found in the creeks. De la Cruz (1965) showed that a number of these species, plus other estuarine fish such as Fundulus spp., Gambusia affinis, Mugil spp., had particulate detritus of salt marsh origin in their guts. He also cites experiments of Kawanabe and Odum which show that Fundulus heteroclitus actually assimilates detritus.

The marshes characteristic of the South Atlantic coast disappear between Jacksonville and St. Augustine, Florida, where mangroves first appear (Davis, 1940a, 1943; Egler, 1952). Where mangroves and salt marsh occur together, the mangroves always occur seaward of the salt marsh, for the mangroves can tolerate deeper water than the marsh plants when established. Egler (1952) suggests that tidal marsh plays the role of pioneer in the mangrove zone, entering after hurricanes and being quickly replaced due to shading by mangroves. The lower west coast of Florida from Tampa southward has a mixture of marsh and mangrove species on sandy flats or marl over limestone flooded at high tide (Davis, 1940a).

Marsh types along the Gulf Coast are composed of essentially the same species as occur along the South Atlantic coast but their proportions are slightly different. Along the Florida coast from Cedar Key to Apalachee Bay there are extensive stands of Juncus roemerianus marsh and the same is true of much of the remainder of the Gulf Coast to Louisiana (Kurz and Wagner, 1957; Hoese, 1967). Spartina alterniflora develops on Florida Gulf Coast beaches where there is limited wave action and in extensive areas along the entire Mississippi coastline, but the more general pattern is broad expanses of Juncus roemerianus marsh grading into upland. The northwestern coast of Florida, from Pensacola to Apalachee Bay, consists mainly of open lagoons and estuaries with little marsh (Hoese, 1967).

The largest expanses of marsh on the Gulf Coast extend around the mouth of the Mississippi (Penfound and Hathaway, 1938; Penfound, 1952; Shiflet, 1963; and Hoese, 1967). Again Spartina alterniflora occupies the areas most regularly flooded by saline water, with brackish marsh of Spartina patens, Distichlis spicata, and Juncus roemerianus covering vast wet areas of lower salinity. A cane zone, dominated by Spartina cynosuroides and Phragmites communis, occurs

at the transition to higher ground where there is a stronger influence of fresh water. Mangroves occur occasionally with Spartina alterniflora in more protected regions of high salinity.

Louisiana marshes are of great importance to the fishery industry of the Gulf. Large zooplankton populations (Figure 17) occur in these marshes and these support sizable populations of predatory fish. In addition, large populations of shrimp and oysters are found in Louisiana marsh systems.

Extensive areas of marsh similar to those in Louisiana occur in eastern Texas where rainfall is greater than evaporation. Spartina spartinae and Sporobolus virginicus are the major species in southwestern Louisiana and along the Texas coast (Penfound, 1952). Small amounts of marsh occur on the shores of bays and on tidal deltas near inlets between Galveston and Corpus Christi (Hoese, 1967). Very limited marshes occur in south Texas but effectively none are present in the hypersaline Laguna Madre because of the stress of high temperatures and salinities (due to low rainfall). There have been studies of the distribution of foraminifera in these marshes (Phleger, 1965) (Figure 18), and the coastal Texas estuarine lagoons, particularly those in eastern Texas, harbor large populations of shrimp (Figure 19).

West Coast Salt Marsh Systems

As indicated, marshes are far less extensively developed along the West Coast. Most marshes form on sediments deposited in small embayments by rivers. In the south these rivers have seasonal flow and those that reach the coast either empty directly into the ocean or into heavily dredged harbors which were once small embayments. Studies of West coast marshes are more limited than those of the East and Gulf coasts.

In southern California, there are several major marsh zones (Figures 20 and 21) present (Purer, 1942, Stevenson and Emery, 1958; Vogl, 1966; Phleger and Bradshaw, 1966b; Bradshaw, 1968). The lower littoral zone is usually a narrow band of Spartina foliosa (leiantha) above which develops a broad belt of Salicornia spp. and Batis maritima. Broad mud flats are exposed below the Spartina belt at low tide. In the upper part of the littoral zone Salicornia spp. continue to dominate but are mixed with many other species such as Monanthochloe littoralis (in drier areas), Distichlis spicata, Limonium californicum, Frankenia grandifolia, and Jaumea carnosa. Farther northward, in San Francisco Bay, a basically similar pattern is found except that Batis is absent (Hinde, 1954). Marshes were originally scattered along the margins of the Bay and apparently never formed a continuous belt. They have been very much reduced in extent recently (Hinde, 1954; Thaeler, 1961). Diurnal fluctuations in environmental factors in a California marsh are shown in Figure 22 and some major plants and animals are illustrated in Figure 23.

Along the Oregon and Washington shorelines, marshes are very limited in extent and little has been written concerning them. They are apparently confined to the borders of some estuaries and to the points of inflow of small streams, as on the Olympic Peninsula. MacDonald (1969) indicates that in Oregon and Washington the upper Salicornia zone is replaced at higher elevations by the tall tussock grass Deschampsia caespitosa.

The distribution of species groups in molluscan faunas (Macdonald, 1969) in Pacific Coast marshes supported Valentine's (1966) concept of southern

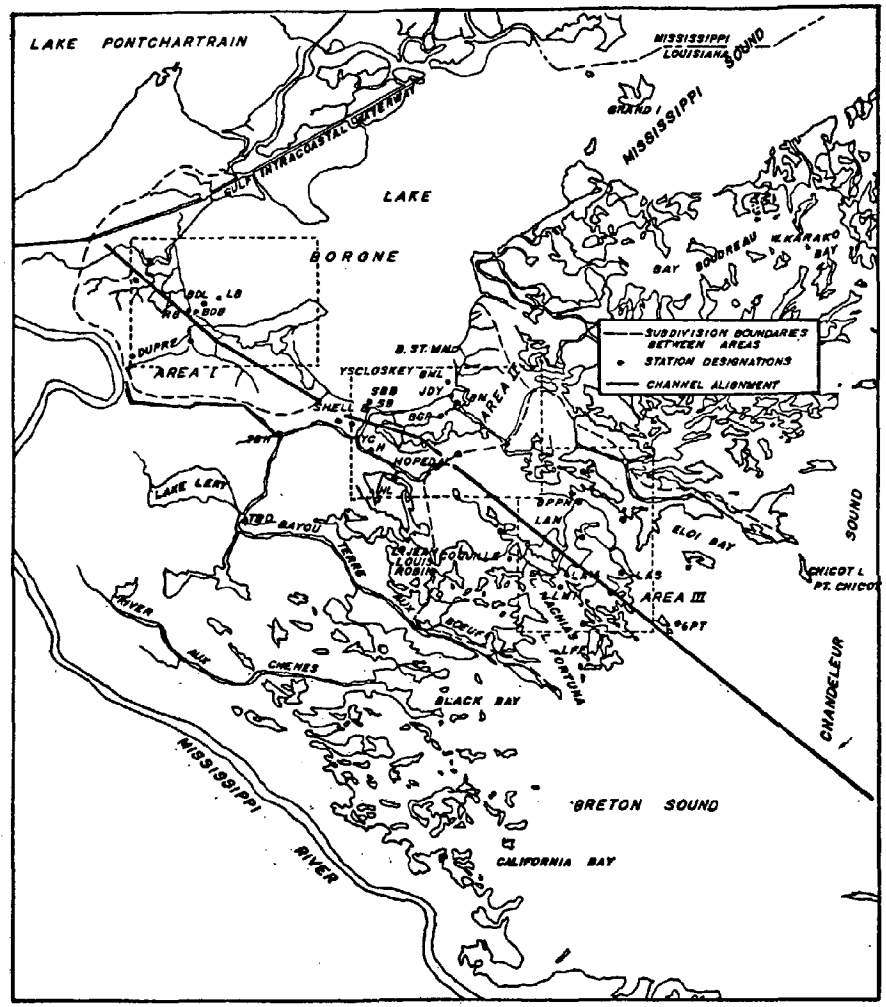
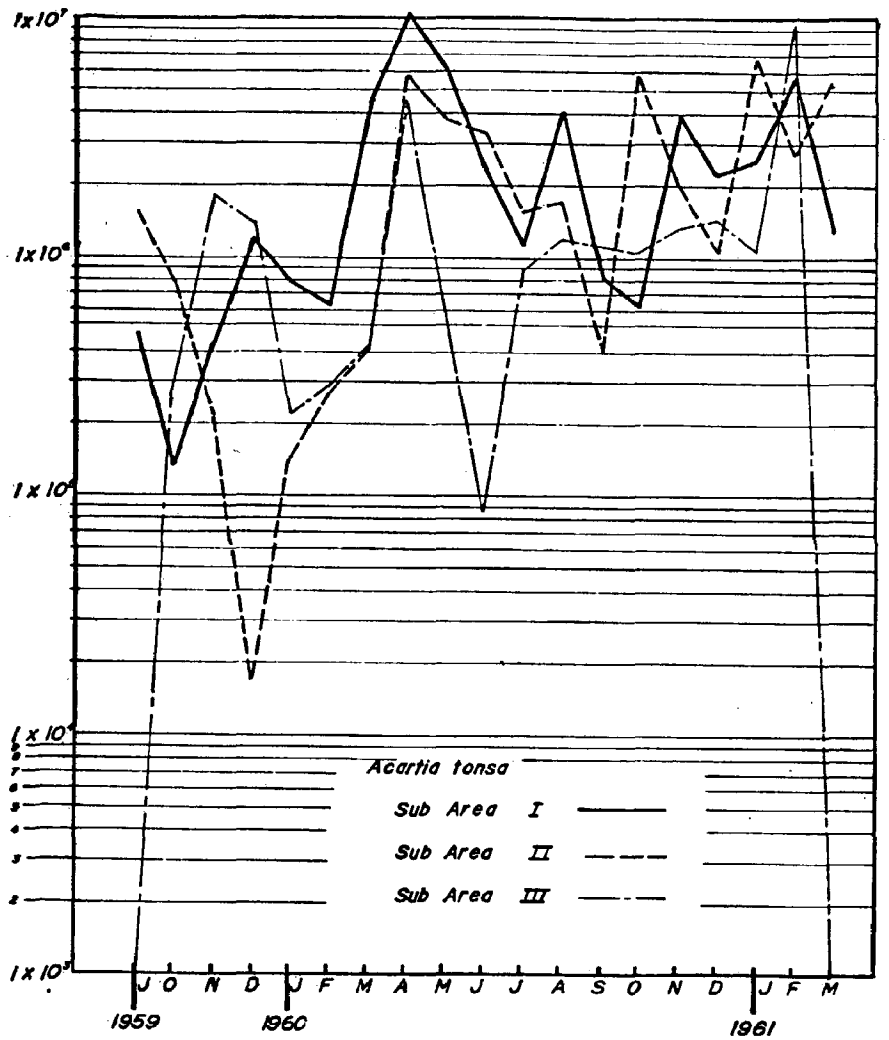
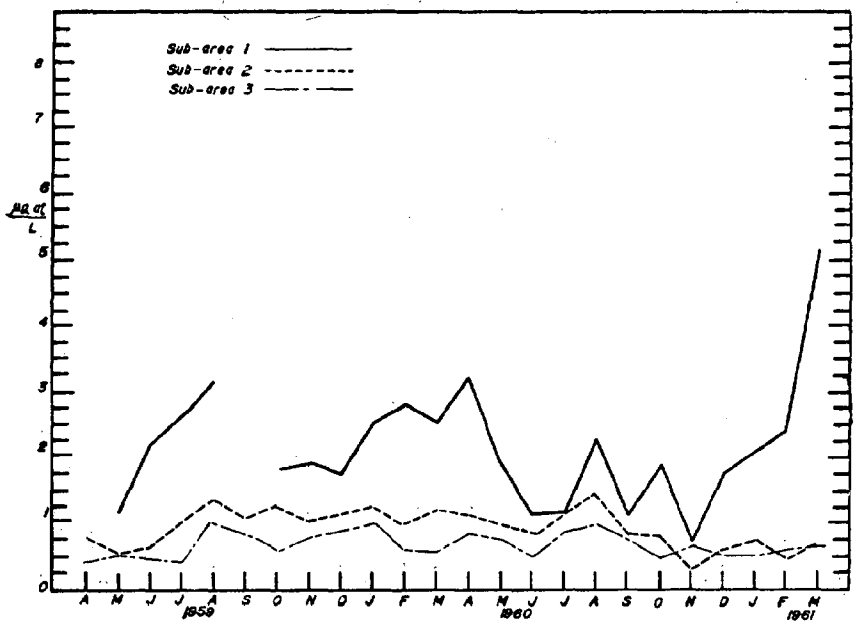


Chart showing the station locations and boundaries of the three sub-areas in the Mississippi River-Gulf outlet project area.

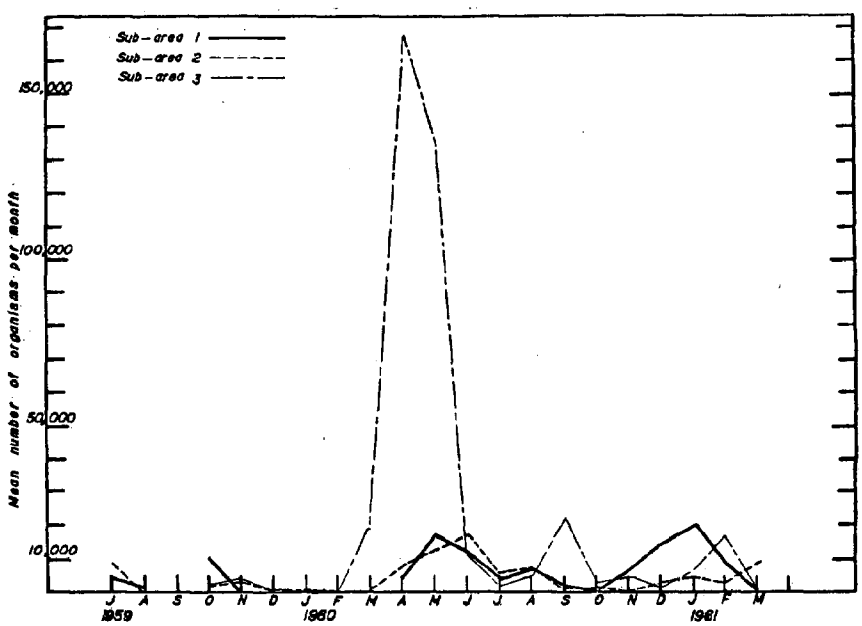


Monthly distribution of *Acartia tonsa* in sub-areas 1, 2, and 3.

Fig. 17A. Planktonic copepods in Louisiana salt marshes (Cuzon du Rest, 1963).

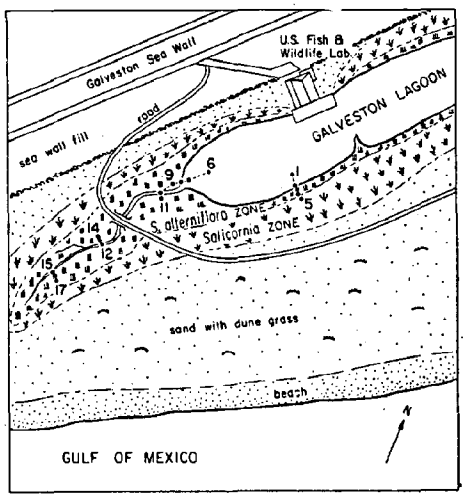


Monthly average inorganic phosphate (µg-at./L) for each sub-area.

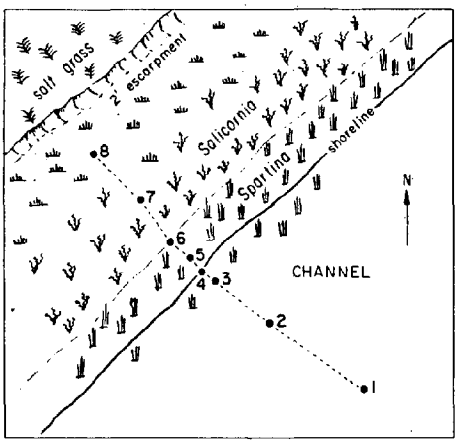


Monthly distribution of the Cirripedia nauplii in sub-areas 1, 2, and 3.

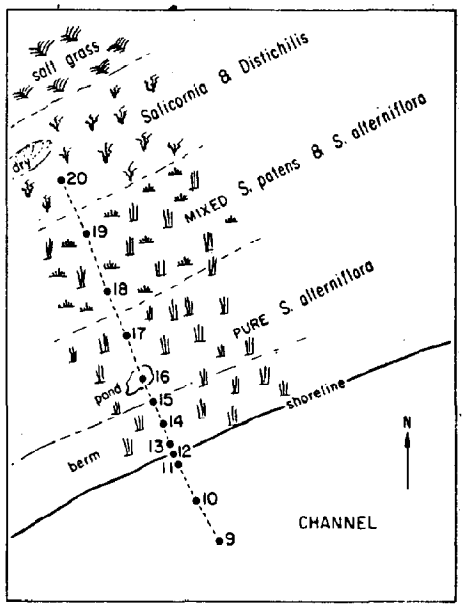
Fig. 17B. plankton nutrients and barnacle larvae in salt marsh waters of Louisiana (Cuzon du Rest, 1963).



Locations of stations in Galveston Lagoon area on Galveston Island.

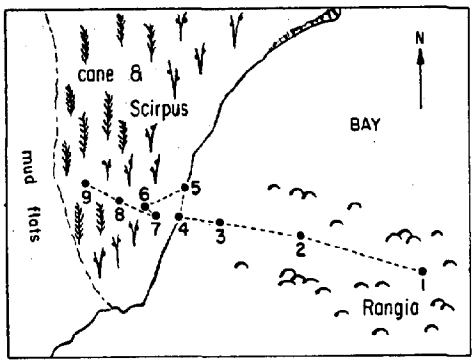


Locations of stations in traverse 1 in lower section of Chocolate Bayou area.

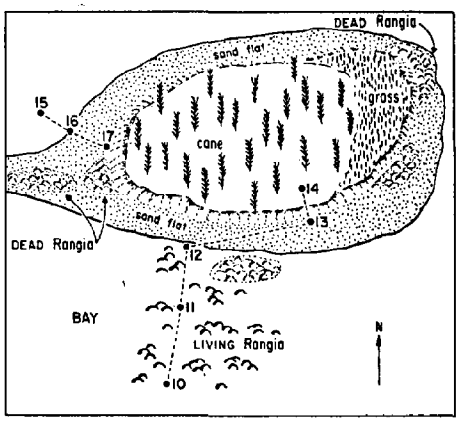


Locations of stations in traverse 2 in Chocolate Bayou area; approximately 2 km upstream from traverse 1.

Fig. 18A. Foraminiferal zones in marsh near Galveston, Texas (Phleger, 1965).



Locations of stations in traverse 1 in Trinity Delta area.

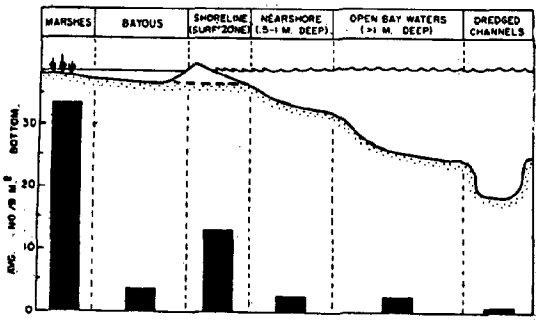


Locations of stations in traverse 2 in Trinity Delta area.

	ADJACENT CHANNEL OR BAY	FRINGING SPARTINA ZONE	SALICORNIA BERM	INNER SPARTINA ZONE	INNER SALICORNIA ZONE	LAGOON BARRIER MARSH	MORE SALINE MARSH	LESS SALINE MARSH
Ammoastuta inepta		— —	— —	— —	— —		— —	—
Ammonia beccarii	—	—	—	—	—	—	—	—
Ammotium salsum	—	—	—	—	—	—	—	—
Arenoparrella mexicana	—	—	—	—	—	—	—	—
Elphidium spp.	— —	— —	—	—	—	—	— —	
Miliammina fusca	—	—	—	—	—	—	—	—
Tiphotracha comprimata		—	—	—	—	— —	— —	—
Trochammina inflata	—	— —	—	— —	—		—	—
inflata var.		—		—				—
macrescens		—		— —	—			—

Generalized distributions of principal marsh species of Foraminifera in Galveston Bay areas arranged according to apparent environments.

Figure 18B. Locations of foraminifera study stations and marsh community zonation near Galveston, Texas (from Phleger, 1965).



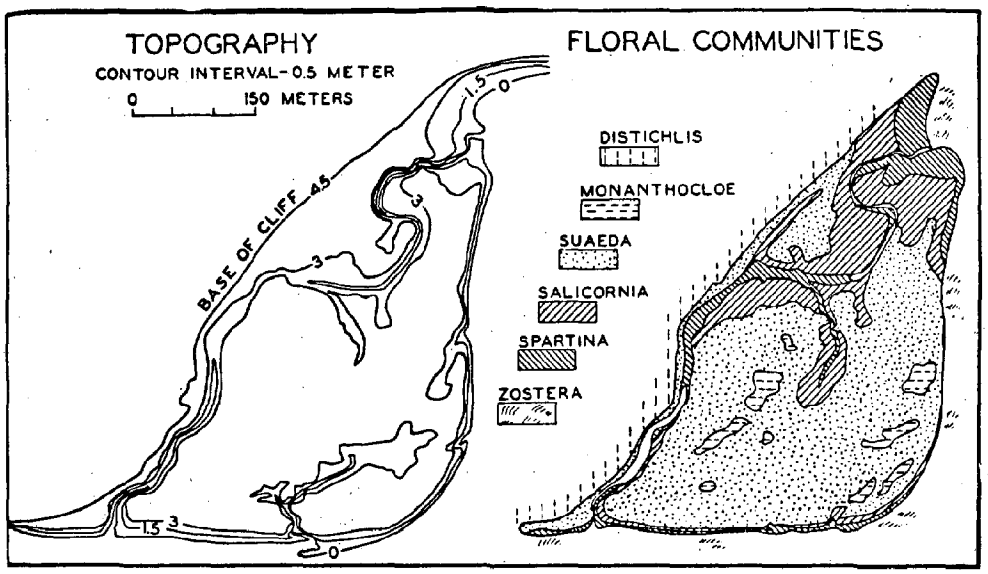
--Relative importance of different types of habitat in the Galveston estuary as nursery areas for juvenile brown shrimp, March-August 1965.

Figure 19. Relative importance of various estuarine habitats as nursery areas for brown shrimp in the Galveston, Texas, estuary (from Chapman, Trent, Mock, Pullen, and Ringo, 1966).

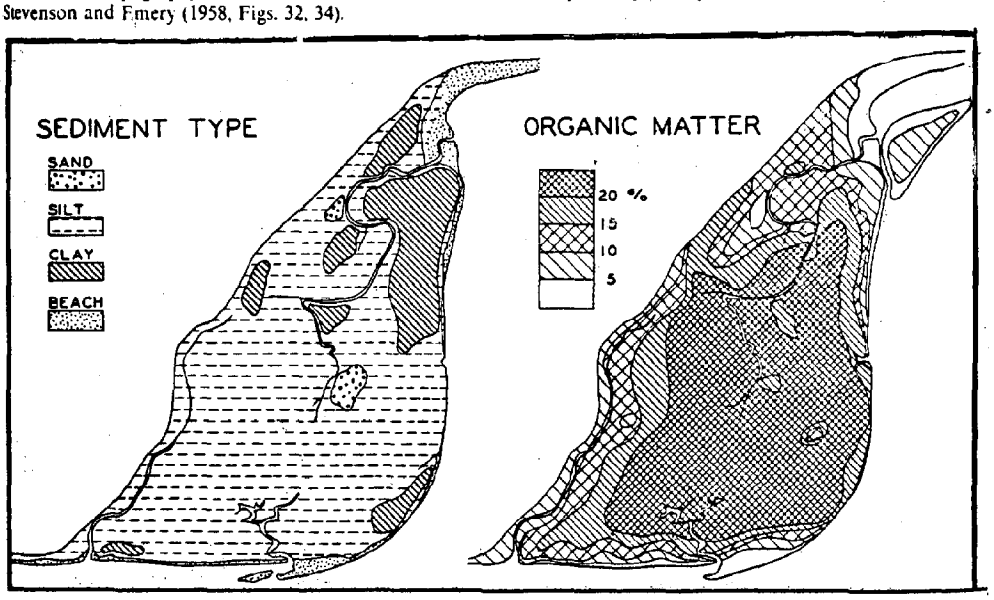
(Californian) and northern (Oregonian) molluscan provinces. Further, the creeks and marshes represented distinct sedimentary environments and had different molluscan faunas. In addition, quantitative features of living faunas were adequately represented in their death assemblages, suggesting that studies of fossil assemblages could yield useful information on evolution of present-day community structure.

SYSTEM FUNCTIONS

The functioning of certain salt marsh systems has been studied as intensively as that of any other natural community. As a result of this research, important generalizations have been drawn concerning both the productivity of natural communities in general and about salt marshes in



Topography and floral communities of marsh at Newport Bay. Adapted from Stevenson (1954) and Stevenson and Emery (1958, Figs. 32, 34).



General sediment types and percentage organic matter of marsh at Newport Bay. Adapted from Stevenson (1954) and Stevenson and Emery (1958, Figs. 31, 36).

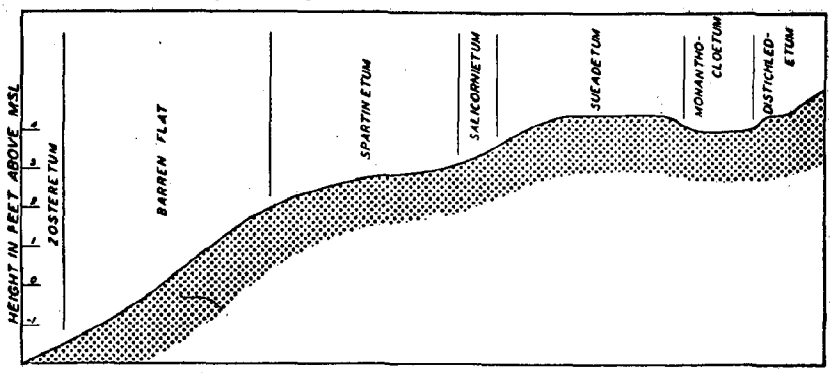
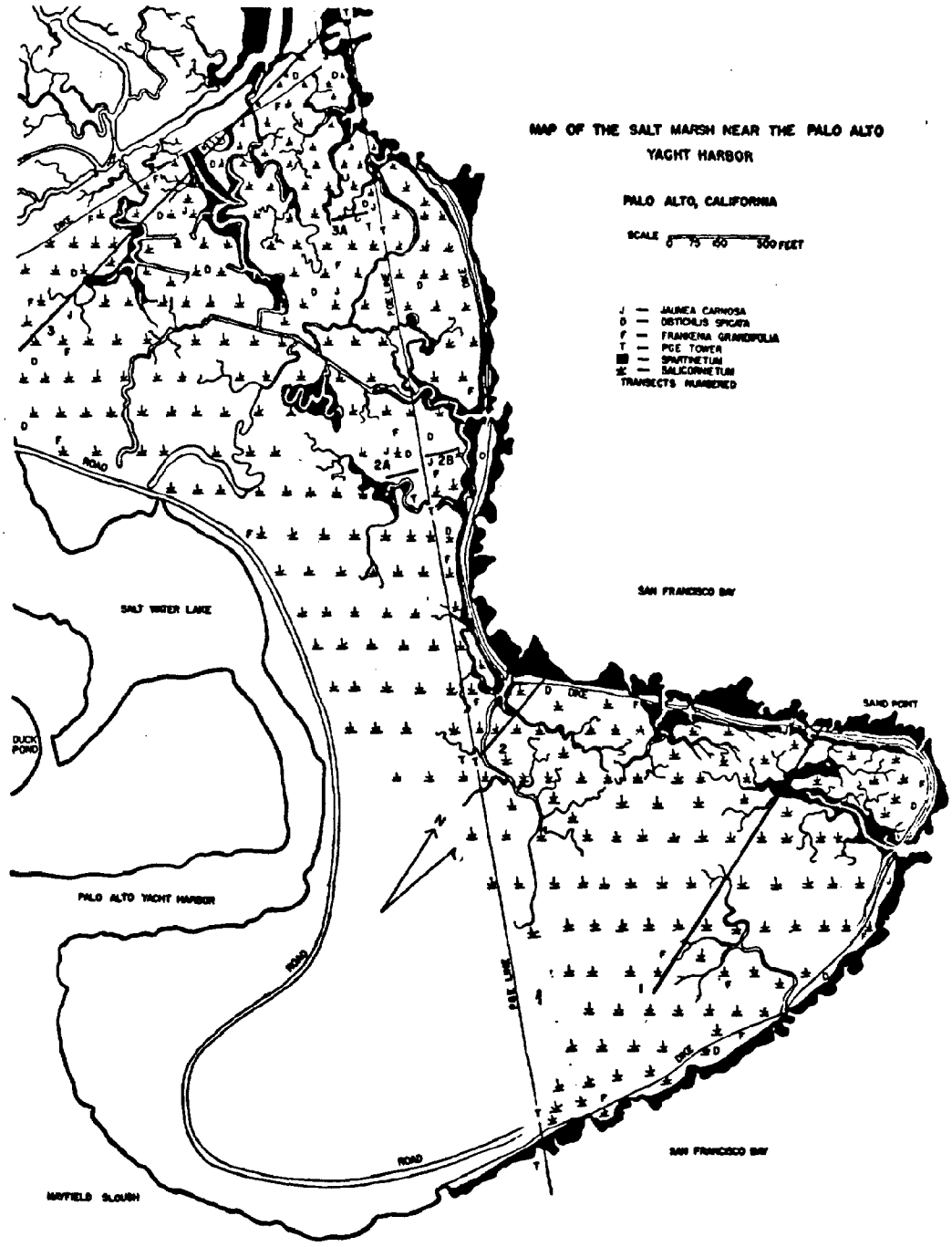
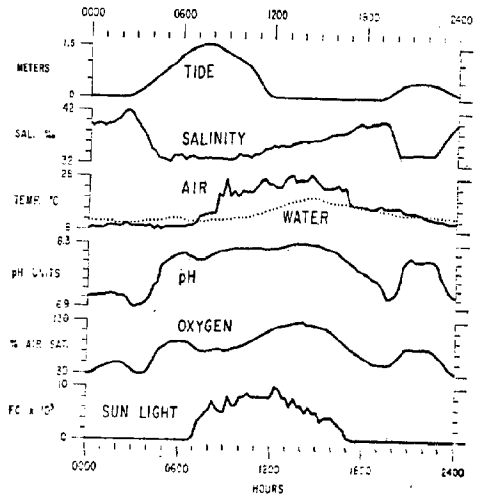


Fig. 20. Topography, community types, sediment types, and organic matter distribution and cross-sectional elevational profile through California salt marsh at Newport Bay, California (Emery, 1960).



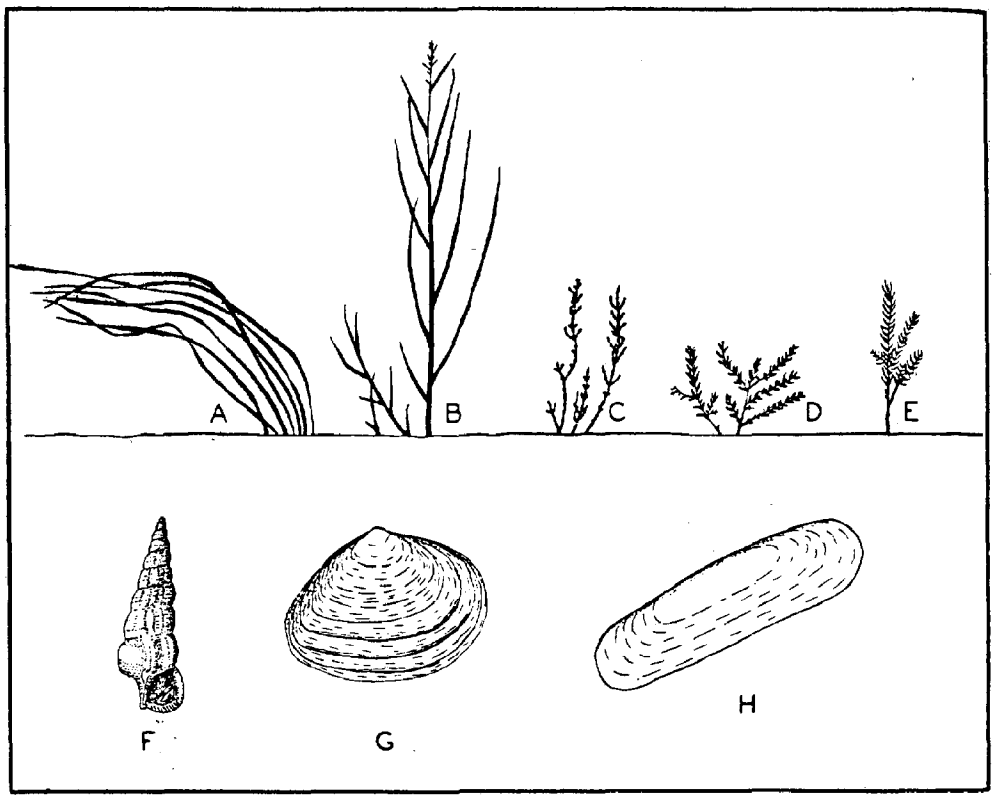
Map of the area showing intricate network of creeks draining the marsh and distribution of dominant flowering plants.

Fig 21. Zonation of community types in California salt marsh near Palo Alto (from Hinde, 1954)



Diurnal variations in environmental factors. (After Phleger and Bradshaw 1966.)

Fig. 22. Diurnal variations in tide, salinity, air and water temperature, pH, oxygen, and sunlight in a California salt marsh (Bradshaw, 1968).



Some important inhabitants of marshes in southern California: A, *Zostera marina* L., eel grass (×0.05); B, *Spartina leiantha* Benth. (×0.05); C, *Salicornia pacifica* Standl. (×0.05); D, *Suaeda californica* Wats. (×0.05); E, *Distichlis spicata* (Torr.) (×0.05); F, *Cerithidea californica* (Haldeman), horn shell (×0.5); G, *Macoma nasuta* (Conrad), bent-nose clam (×0.8); H, *Tagelus californianus* (Conrad), jackknife clam (×0.5).

Fig. 23. Some important plant and animal species found in California salt marshes (Emery, 1960).

specific. The data available on system metabolism come almost exclusively from the South Atlantic type of salt marsh, described in detail earlier. These studies show that, at least in the case of the Spartina alterniflora-dominated low marsh, the marsh is an integral part of the estuary (Odum, 1961b). The marshes provide food and shelter, not only for organisms naturally inhabiting the marsh, but also for many organisms which spend their lives in the waters of the estuary and adjacent shallow ocean.

The first, and to date most complete, studies of salt marsh productivity have been conducted at Sapelo Island, Georgia. These studies provide quantitative estimates of productivity and energy flow in low Spartina alterniflora marsh and undoubtedly can provide a framework for interpreting similar processes in salt marshes elsewhere. The following summary is adapted from Teal (1962), Smalley (1959, 1960), Odum and Smalley (1959), and others as indicated.

Primary production is carried out by two groups of plants, the marsh grasses and the algae living on the surface of the marsh mud. In the Georgia marsh, Spartina alterniflora is the only grass of importance. Along the creeks where it grows in its tall form the grass productivity is greatest, averaging over three times that of the short grass in the higher marsh. Net production along creeks was found to average over 2200 $g/m^2/yr$ (8970 $kcal/m^2/yr$) whereas net production of short grass was 643 $g/m^2/yr$ (2570 $kcal/m^2/yr$). Based on the relative areas of the two marsh types, net primary production over the marsh as a whole averaged about 1600 $g/m^2/yr$ (6850 $kcal/m^2/yr$). Respiration of the marsh grass is very high, amounting to an average of 28000 $kcal/m^2/yr$ for the entire marsh (Teal and Kanwisher, 1961). Thus, gross production of the marsh grass averaged about 34600 $kcal/m^2/yr$ over the marsh. This gross production (6.1% of the 600,000 $kcal/m^2/yr$ of incoming solar energy) represents a rather high efficiency for a natural community. However, the high respiration, over 75% of gross production, reduces net production to only 1.4% of incoming light energy. This is still a rather high value in comparison to other natural communities. The mud algae have an annual gross productivity of about 1800 $kcal/m^2/yr$ of which about 180 go into respiration. Thus, the algae contribute a net production of about 1600 $kcal/m^2/yr$ (Pomeroy, 1959). Total net production for the marsh therefore, is somewhat over 8200 $kcal/m^2/yr$, or approximately 2000 $g/m^2/yr$ biomass.

Two major groups of animals utilize this net production (Figure 10). Grasshoppers and plant hoppers feed directly on the marsh grass and these in turn are eaten by spiders and smaller birds such as sparrows. Total energy flow through this grazing chain is very small as only 305 of the 6500 kcal (about 5%) of gross production are utilized by the insects.

The vast majority of energy moves through the detrital food chain (Figure 10). Here, the dead leaves and stems of Spartina alterniflora are broken down by bacteria in the creek waters and on the surface of the marsh. Estimates suggest that bacterial degradation of Spartina alterniflora amounts to almost 60% of that available with bacterial respiration amounting to almost 4000 $kcal/m^2/yr$. In breaking down the cordgrass remains, the bacteria actually increase the food value of the detritus as the cellulose content decreases most rapidly and the protein content least rapidly. The

detrital particles and mud algae are eaten by a variety of detritus feeders, such as fiddler crabs, nematodes, snails, and mussels. These organisms are, in turn, eaten by mud crabs, rails, and racoons (Figure 10). A total of about 460 kcal/m^2/yr move into this feeding sequence. This leaves a significant portion (almost 90%) of the 4000 kcal in the detritus-algae category after bacterial action unutilized. This detritus, augmented slightly by contributions of dead matter from the primary and secondary consumers, is washed from the marsh as new export. Thus, 3670 kcal (45%) of the original 8200 kcal of net primary production are not used by the marsh organisms and become a significant portion of the energy budget of the detritus and filter feeding organisms which live in the estuary. This exported detritus, plus plankton, feeds the myriads of larval and mature fish and shellfish which utilize the estuarine waters. Ragotzkie (1958) has shown that, because of the high turbidity of the estuarine waters in Georgia, net production of the plankton algae is zero. Thus, in these waters, detritus must form the major basis of food for estuarine animals.

Teal, in summarizing his energy flow picture of the Georgia marsh (Figure 12), indicated that these marshes are extremely stable, at least over the period of time studied. He points out that, according to MacArthur (1955), a community may achieve stability by having either many species with rather restricted diets or few species with broad diets. The salt marsh has evolved toward the second, and less common, alternative. This appears to be true because there is only one higher plant in the marsh (Spartina alterniflora), with a consequent lack of possible niches, and because of the constant removal of biomass by tidal currents.

Following Teal's summary of system energy flow, the detrital metabolism of the Spartina alterniflora marsh has been studied in detail by de la Cruz (1965) and Marples (1966). De la Cruz' study dealt with various aspects of the formation of detritus, movement into tidal creeks, and its utilization by marsh and estuarine consumers. He found that 90% of the detritus originated from Spartina grass and that there was always more suspended organic matter present at mid-ebb tide (an average of 20 mgm/l) than on mid-flood tide (an average of 5 mgm/l), indicating a net export of detrital material from the marsh. This detritus was over 95% nanno detritus and standing crops of 2-20 mgm ash-free dry organic matter per liter were recorded. There was also evidence that the organic fraction of the nanno detritus was richer in protein than the grass from which it came and thus was potentially a better food source than the original Spartina tissue. Semi-qualitative estimates of the stomach contents of a number of marsh, estuarine, and coastal animals revealed that organic detritus, mostly of Spartina origin, was of frequent occurrence. In at least one species (Fundulus heteroclitus) unpublished research of Kawanabe and Odum indicates that detritus is assimilated. Further studies will be necessary to determine if the detritus particles serve a nutrient role in other species and whether the source of nutrition is the organic substrate or the associated microbiota or both. Marples' work dealt with arthropod and associated food chains in the marsh proper. Using radioactive tracers he established that there is a group of grazers (grasshoppers and leaf hoppers) which eat only living Spartina. Another group of arthropods fed primarily on detritus from the marsh surface. This group also included the snail Littorina and the small crabs Uca and Sesarma. A final group of arthropods was identified and this included

predators of which spiders were the largest in number. The position of certain other species, such as ants, was not entirely clear.

Another study of importance dealt with mussel populations (Kuenzler, 1961a, 1961b). Here the importance of this species to the phosphorus budget of the marsh was shown. The major effect of the mussels upon the phosphorus budget lay in their rapid removal of particulate organic matter from the water and its deposition on the marsh surface where it is utilized by the many deposit feeders. Thus, the mussels, although they are of limited importance in terms of energy flow are quite important in maintaining the fertility of the marsh.

There are no studies elsewhere along the Atlantic Coast comparable in their detail to those on Sapelo Island. Thus, it is not possible to assess the degree to which the various directions and magnitudes of energy flow may vary geographically. There are, however, some additional studies in the southeast of primary productivity in salt marshes and these data may be used as a basis for generalizations concerning salt marshes in other areas.

The most extensive studies are those of Williams and Murdoch at the U. S. Fish and Wildlife Service Radiobiology Laboratory at Beaufort, North Carolina (Williams, 1965b; Williams and Murdock, 1966a, 1966b, 1966c). The purpose of these studies has been to determine the contributions to net primary production made by each of the major groups of producers in the shallow estuaries around Beaufort. The groups considered are the phytoplankton, submerged aquatics (primarily Zostera and Ruppia), marsh plants, and benthic algae. Data are available for the first three groups. Williams has approached his problem by determining rates of production for the various groups of plants involved and then determining the area occupied by the ecological group in question. With these data, it is then possible to estimate the total contribution which an ecological group makes to the estuary.

The average annual dry weight production of all height forms of Spartina alterniflora was 640 g/m^2. This represented 256 g $C/m^2/yr$ or about 2560 $kcal/m^2/yr$. Several progressive refinements of studies of net production in Juncus roemerianus suggest that its annual net production is 735 g/m^2 (Williams and Murdoch, 1968), or approximately 2940 $kcal/m^2/yr$. Thus, it appears that the annual net production of Spartina alterniflora and Juncus roemerianus in this area is approximately equal. The marshes surrounding the sounds in the Beaufort area were estimated to cover about 166 km^2. Of this area, 74 km^2 was Spartina alterniflora and 79 km^2 Juncus roemerianus, the remaining 13 km^2 being either high marsh, ponds, or other miscellaneous types. Williams assumes that only Spartina alterniflora makes any significant contribution to the energy budget of the estuary as it alone lies within the normal zone of tidal fluctuation. Juncus roemerianus, on the other hand, lies above normal tidal influence and there most decomposed material goes into peat formation in place. Unpublished work in the same area by Byron supports this view. He has found that there is essentially no change in the standing crops of suspended organic matter in the flood

and ebb tides in creeks draining two areas of Juncus marsh. There was, in fact, a 40% reduction in the amount of nitrogen in the ebb tide as compared to the flood tide, suggesting that these marshes are, in fact, nutrient sinks. Placing the annual net production of Spartina onto an area basis, indicates that there was an annual net production of carbon equal to 19,000 metric tons for the entire estuary. Similar studies show that phytoplankton contribute 21,500 metric tons carbon per year and submerged aquatics perhaps as much as 20,400 metric tons carbon per year. Thus it appears that each of these three ecological groups makes an approximately equal contribution, roughly 20,000 metric tons carbon per year, to the Beaufort area estuaries. By comparison with the data from Sapelo Island, it can be inferred that the proportional contribution by the marsh is less in the Beaufort area, due in part to lower plant production over a smaller area of marsh and in part to the clearer water which permits greater production by phytoplankton and submerged aquatics.

Similar studies have been carried out by Stroud (1969) in Spartina alterniflora marsh at the mouth of the Cape Fear River in Brunswick County, North Carolina. Here the best estimates for annual net production of Tall Medium, and Short Spartina were 1562, 471, and 280 g/m^2 respectively. Juncus averages 1306 $g/m^2/yr$. Average production for Spartina alterniflora throughout the entire marsh was 646 $g/m^2/yr$, or 2586 $kcal/m^2/yr$., a figure very close to that determined at Beaufort by Williams. Working in the same general area Foster (1968) found annual net production of Juncus to range from 560 - 1000 g/m^2. In this marsh, Tall, Medium, and Short Spartina covered 44%, 10% and 6% of the marsh, respectively, while Juncus covered about 9%. The remaining 31% was creeks, mud banks, and spoil areas.

There has been one study of net primary productivity in irregularly-flooded marsh (Waits, 1967). This study was carried out on the North Carolina Outer Banks in a marsh with four community types present: a type dominated by Spartina patens; a Mixed Type in which Spartina patens, Distichlis spicata, and Scirpus robustus dominated; a Juncus roemerianus Type; and a Marginal Type at the marsh periphery. The best available estimates indicate that net primary production in the Spartina patens type was 1367 $g/m^2/yr$ (6152 $kcal/m^2/yr$), in the Mixed Type 984 $g/m^2/yr$ (4428 $kcal/m^2/yr$), in the Juncus Type 895 $g/m^2/yr$ (4028 $kcal/m^2/yr$), and in the Marginal Type 399 $g/m^2/yr$ (1796 $kcal/m^2/yr$). Production over the entire marsh averaged 961 $g/m^2/yr$ (4324 $kcal/m^2/yr$). Thus, it appears that net annual community production in irregularly-flooded marshes may equal or exceed that of certain low marshes, particularly those in which there is a high percentage of the relatively unproductive Short Spartina alterniflora relative to the total area of the marsh. However, the best information at the moment, supported by fragmentary data such as those of Byron (1969), indicates that the vast majority of this production goes into peat production and remains in the high marsh rather than being exported.

There are now enough data to determine, at least in a preliminary way, geographic relationships of production in Spartina alterniflora on the east coast (Table 1). When the studies in Georgia and North Carolina are compared with studies in Delaware (Morgan, 1961) and New Jersey (Good, 1965) it is apparent that annual net production of Spartina alterniflora decreases with latitude. In Georgia, biomass production over the entire marsh averaged 1600 $g/m^2/yr$. In the North Carolina studies similar values were 646 in

Table 1

Comparison of Atlantic Coast data for net primary production of *Spartina alterniflora* from selected localities

	Tall Spartina	Medium Spartina	Short Spartina	Marsh Average
Georgia (Teal, 1962)				
% of marsh	20	35	45	
Net primary prod. ($g/m^2/year$)	2200		643	1600
Net primary prod. ($Kcal/m^2/year$)	8970		2570	6850
North Carolina--Brunswick Co.				
% marsh	6	10	44	
Net PP ($g/m^2/year$)	1563	471	280	646
Net PP ($Kcal/m^2/year$)	6471	1856	1106	2590
North Carolina (Williams)				
Net PP ($g/m^2/year$)		640		640
Net PP ($Kcal/m^2/year$)		2560		2560
Delaware (Morgan, 1961				
Net PP ($g/m^2/year$)		361		361
New Jersey (Good, 1965)				
Net PP ($g/m^2/year$)		325		325

Brunswick County and 640 farther north at Beaufort. Delaware and New Jersey figures were 361 and 325 respectively. The primary factor operative seems to be a latitudinal effect on length of growing season. In Georgia, Spartina grows throughout the entire year and, to a more limited extent, it does so in North Carolina. In Delaware and New Jersey, production is limited to the growing season from late April through September (Morgan, 1961; Good, 1965). The degree to which export of organic matter from Spartina alterniflora marshes other than those in Georgia occurs is open to speculation. It is reasonable to suppose that in areas with similar tidal regimes a very high percentage of the total marsh production goes into the export pathway.

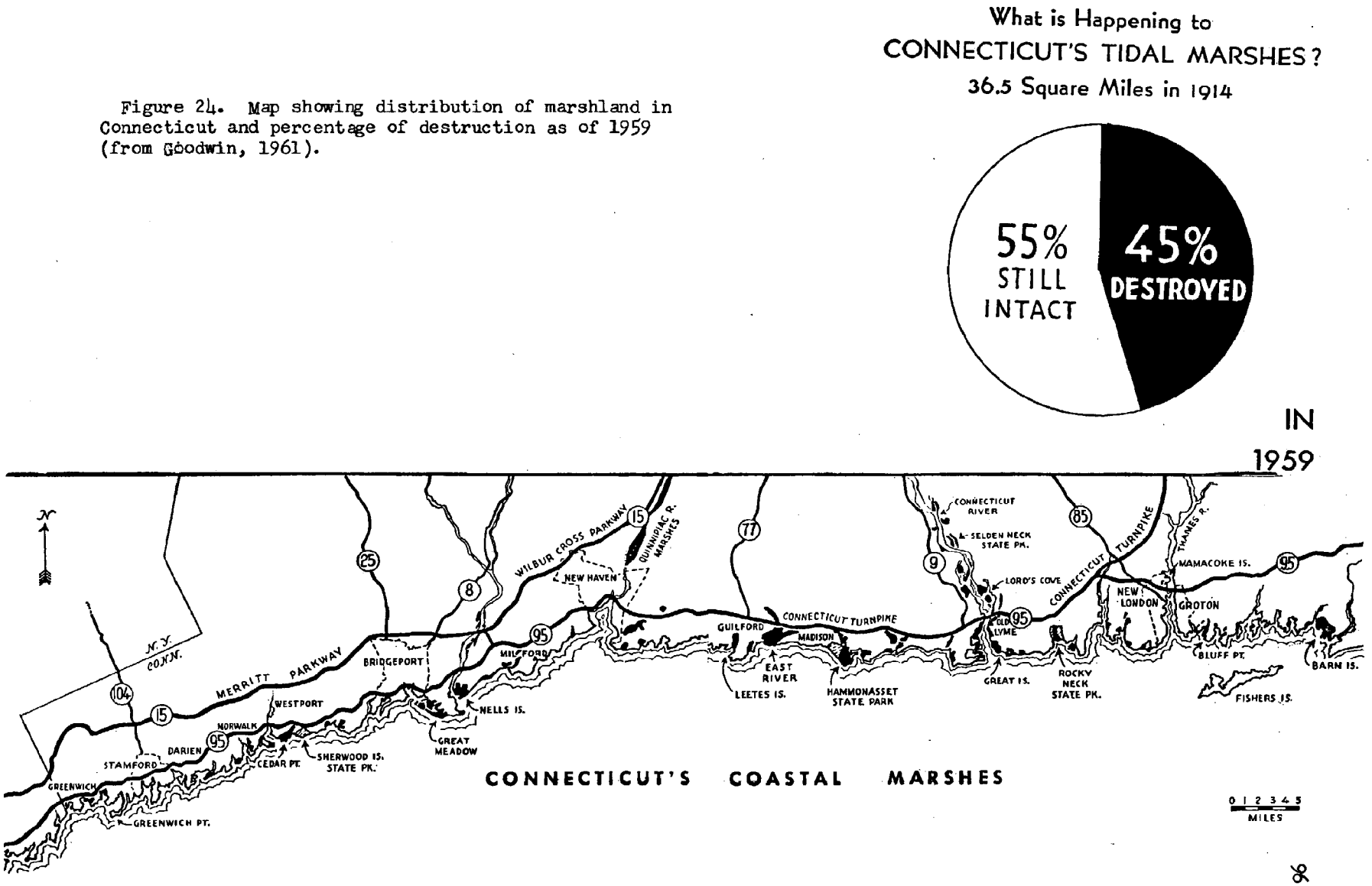
EFFECTS OF STRESSES ON THE SALT MARSH ECOSYSTEM

Salt marshes are subject to a great variety of stresses which alter, or threaten to alter, the natural marsh system. In some cases the effects of these stresses on the marsh are clear and documented, but in the majority there are few data despite the fact that the stress may be obviously detrimental to the marsh system.

Perhaps the most obvious and clear cut destructive forces are those which fall under the general category of dredge and fill, channelization, and spoiling. These may be associated with improvement of navigation, with development of commercial or residential land, or with refuse disposal. In all cases, there is virtually total destruction of marsh habitat as it is filled with silt or sand or refuse to an elevation at which marsh can no longer survive. Thus, the effects of spoiling in the estuarine environment can best be assessed in terms of direct physical loss of habitat (Chapman, 1968). Schmidt (1966) reports that 45,000 acres of tidal marsh were destroyed between Maine and Delaware from 1954 to 1965. Spoiling from dredging of channels and harbors accounted for 34% of this loss. In 1959, 45% of Connecticut's 36.5 square miles of marsh had been destroyed (Figure 24). In North Carolina alone (Burdick, 1967) 46,000 acres of marsh have been altered between 1952 and 1967. The greatest percentage of this was due to dredging and channelization for mosquito control or land development. Similar figures could be quoted for other areas. In the case of most dredging, it is clear that the marsh system, and its values, are destroyed and replaced by an entirely different system.

Two ramifications of dredging and spoiling need to be considered. In many cases, spoiling results only in run-off of materials onto marsh land rather than in a whole-sale destruction of marsh by increased elevation. A case of run-off from dredging of the Intracoastal Waterway occurred in North Carolina in 1965. In this situation, a large area was covered with black silt and clay. Immediate effects were a complete destruction of oysters, clams, and crabs on site. Although the marsh grass appeared affected at the time, subsequent tidal action appears to have re-distributed some of the material and the marsh is now in reasonably good condition. In a case such as this, where effects of siltation are sufficiently limited that the dominant marsh plants can persist, it appears that the system can survive the stress and re-generate. It should be emphasized, however, that this comment is based only on observation.

Figure 24. Map showing distribution of marshland in Connecticut and percentage of destruction as of 1959 (from Goodwin, 1961).



The other aspect of dredging of interest is the possibility of construction of new marshland on dredging spoil. Considerable interest in this area has arisen recently as a result of desire to stabilize dredging spoils and to construct new habitat. It would appear feasible to construct new marshland if methods of spoil deposition can be achieved which permit formation of a surface at a precise elevation. Given proper elevation there seems no reason why natural or artificial regeneration of marsh species could not be employed. Construction of new marsh land should be viewed with caution, however, for it is clear that to construct new marshes some other estuarine land, perhaps equally valuable, must be used. There is little merit in destroying one habitat to build another.

Another major stress on salt marshes is activity associated with the control of salt marsh mosquitoes. These insects breed in areas of salt marsh which are intermittently flooded, such as the high marsh, and can create serious discomfort and health problems in the coastal area. Of the many methods used to control salt marsh mosquitoes, two involve habitat manipulation. These are drainage by ditching and flooding by construction of dikes. In the case of ditching, the purpose is to dry out the marsh and thus reduce periods of standing water which induce egg hatching. In a study of the effects of ditching in Delaware Bourn and Cottam (1950) showed that there was indeed a marked "drying out" of the marsh and that this had pronounced effects on the marsh system. Spartina alterniflora marsh covered 90% of the study area in 1936 when ditching was begun. Five years later it had been almost entirely replaced by shrubby species such as Baccharis halimifolia and Iva frutescens. In addition populations of insects, molluscs, and crustaceans were drastically reduced, in some cases over 90%. In this case, the effects on the system are clear. As a result of ditching, water tables were lowered and duration of flooding reduced and, consequently, the species populations shift toward those more characteristic of drier situations at the edge of the marsh. The habitat and biota become more like those of the highmarsh border system, which is characterized by smaller numbers of animals (Davis and Gray, 1966) and essentially no export of organic matter to the estuarine waters. Thus, the effect on the marsh proper and the estuary is probably detrimental.

A note of caution must be injected here concerning ditching. The case described above involves ditching and drying of what was originally salt marsh regularly flooded by tides. It seems clear that this is seriously detrimental, both to the marsh system and to the estuary. In the case of ditching in marshes which are irregularly flooded by tides, the answers are not so clear. Although there is some evidence that ditching in these systems may dry them out it also seems that the increased edge and tidal penetration may increase productivity and contact with the estuarine waters. This is clearly a subject which needs research.

In the case of diking, the results are quite different (Provost, 1968). As carried out extensively in Florida and New Jersey, it consists of diking areas of marsh above the normal high tide line and impounding fresh or brackish water. In Florida impoundments, shrubby marsh of Batis, Salicornia, Suaeda, and Monanthochloe is eliminated and replaced either by freshwater species such as Typha and Scirpus or by low marsh species if the water is brackish. In this case it seems clear that a rather non-productive habitat (in terms of total life) is replaced by a much more productive one.

Impoundments become favorite bird habitats and, in many cases, large and desirable fish populations are developed. The system is closed, in the sense that there is no opportunity for tidal interchange, but this was virtually absent in the natural state. In the case of diking it appears that a new, more productive system is substituted for the natural, less productive system.

Pesticides are another stress which is affecting salt marsh systems. This subject is covered in detail in other papers in this volume and therefore will be mentioned briefly here. As in most cases of pesticide application, it appears that salt marsh organisms occupying relatively high positions in food chains are those most affected. Springer (1961) summarizes work done between 1949 and 1952 on the effects of DDT and aldrin in oil and DDT, aldrin, dieldrin, and BHC in granules on tidal marsh systems on the east coast of the United States. Of all the animals studied, arthropods were affected the most seriously by DDT. Prawns and blue crabs were particularly affected. Fish in marsh creeks suffered heavy mortality at high dosage levels but only small losses at lower levels of dosage. Molluscs, snails, turtles, frogs, and mammals showed little evident harm. BHC was by far the most toxic to crabs of the four insecticides applied in granular form. Woodwell et. al., (1967) report a study of pesticides in a Long Island *Spartina patens* marsh. In this study, increasing concentrations of pesticide with increasing trophic levels were established. It is clear that pesticides represent a major potential stress on salt marsh systems and that their major effects will be felt first in the organisms highest in the food chains.

Many other stresses affecting salt marsh systems have been mentioned. These include increased salinity due to navigation improvement projects and to natural land subsidence, erosion related to natural sea level rise or land subsidence, thermal pollution, phosphate mining, and many others. There are few studies available of the specific effects of any stress on a salt marsh system. Although it might be possible to synthesize a model, from available data, to describe the effects of certain stresses on the system, it seems that we are, as yet, far removed from this goal.

Chapter G-4B

TIDAL MARSHES OF DELAWARE

Franklin C. Daiber

with sections by
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INTRODUCTION

A studied example of a salt marsh system showing tidal creek interactions is the Broadkill River Estuary of Delaware (Fig. 1) studied by class teams of the University of Delaware. Representative graphs are given here from reports and theses.

Equidistant hydrographic stations were established along the creeks as shown in Fig. 1, and samples for salinity and other variables were taken at spring tide and neap tide conditions. As shown in the representative Fig. 2 high salinity penetrated approximately the full length of the small creeks and about 3 miles upstream in the larger creeks (Daiber and de Witt, 1968).

The important role of marshes as nurseries in providing food chains for fishes was established by sampling waters for planktonic fish eggs and larvae (icthyoplankton).

A biweekly night-time mid-flood sampling program was carried out over 15 months on three tidal streams that spanned the length of Delaware Bay and the lower river. One-half hour collections were made by suspending 12 inch No. 0 mesh nets in the flooding current, surface, and bottom. The movement of the tidal front was such that these three streams, Canary Creek, Little River, and the Appoquinimink Creek could be sampled successively during a single flooding tide. Another sampling program during the summer of 1962 involved one-half hour collections each hour over 6, 12, 24, and 48 hours using the same nets.

There was a seasonality in abundance of fish eggs and larvae in three Delaware tidal creeks. The majority were taken during June and July. Most of the eggs and larvae were taken in the higher salinity waters of the state. Larger numbers were taken during the night hours during high salinity periods of the tidal cycle than at other times. One of the graphs is Fig. 3.

The forage species such as the anchovy and silversides are the most abundant species in the net samples (Tables 1 and 2). These fish larvae and eggs are carried into the creeks on the flooding tides and flushed from the streams as the tide ebbs. Large numbers may be stranded in the marsh or eaten, as fewer are caught on the ebb than on the flood tide (Fig. 3).

Table 1. Species composition of fish larvae identified from the biweekly mid-flood plankton collections from June 1961 into September 1962.

SPECIES	CANARY CREEK	LITTLE RIVER	APPOQUINIMINK	TOTAL
Anchoa	1365	90	114	1569
Menidia	57	240	16	313
Fundulus	16	59	2	77
Anguilla	13	22	11	46
Gobiosoma	16	5	3	24
Pleuronectidae	-	8	1	9
Roccus	8	0	2	10
Brevoortia	-	-	1	1
Syngnathus	1	3	0	4
Sciaenidae	5	1	0	6
Bairdiella	4	0	0	4
Clupeidae	0	3	0	3
Unidentified	7	2	1	10

Table 2. Percentage distribution of catch of fish larvae taken during the summer of 1962 excluding biweekly mid-flood samples.

Sample Duration	6 hr.				12 hr.		24 hr.						48 hr.	
Date of Sample	20/6	25/6	28/6	2/7	19/7	19/7	21st June			5th July			6-8 June	Grand Aver.
Location / Species	Canary Creek				Can. Creek	Little River	Can. Creek	Little River	Appo. Creek	Can. Creek	Little River	Appo. Creek	Can. Creek	
Anchoa mitchilli	83.70	48.08	75.99	98.38	60.93	44.68	51.95	38.46	59.85	96.13	44.76	73.86	88.15	82.28
Menidia sp.	11.48	21.15	25.00	0.46	11.92	17.02	40.23	28.20	29.20	0.62	23.62	12.03	8.75	9.90
Fundulus sp	1.24	-	-	0.23	20.53	27.66	1.95	25.13	2.19	0.57	4.44	4.15	2.56	3.02
Gobiosoma sp.	0.15	3.85	-	0.23	2.65	5.32	2.34	4.61	5.11	0.67	25.40	7.88	-	2.70
Sciaenidae	1.83	9.62	-	0.70	0.66	-	2.73	0.51	-	0.47	-	-	0.44	0.79
Bairdiella chrysura	0.95	11.54	-	-	-	1.06	0.39	2.05	1.46	1.38	0.35	-	-	0.74
Syngnathus fuscus	0.29	3.85	-	-	1.32	-	-	-	-	0.04	0.89	-	0.04	0.19
Pomolobus aestivalis	0.07	-	-	-	-	-	-	1.02	-	-	-	-	-	0.04
Centropristes striatus	0.15	-	-	-	0.66	-	-	-	-	-	-	-	-	0.04
Prionotus sp.	-	1.92	-	-	1.32	-	-	-	-	-	-	-	-	0.04
Clupeidae	0.07	-	-	-	-	2.13	-	-	-	-	-	-	-	0.04
Roccus sp.	-	-	-	-	-	-	-	-	-	0.09	-	-	-	0.03
Brevoortia tyrannus	-	-	-	-	-	-	-	-	1.46	-	-	-	-	0.03
Menticirrhus sp.	-	-	-	-	-	-	-	-	-	-	-	-	0.04	0.01
Hyporhamphus unifasciatus	-	-	-	-	-	-	-	-	-	-	0.18	-	-	0.01
Pseudopleuronectes americanus	-	-	-	-	-	-	-	-	-	-	0.18	-	-	0.01
Strongylura sp.	-	-	-	-	-	-	-	-	0.73	-	-	-	-	0.01
Spheroides maculatus	0.07	-	-	-	-	-	-	-	-	-	-	-	-	0.01
Unidentified	-	-	-	-	-	2.13	0.39	-	-	-	0.18	2.07	-	0.11

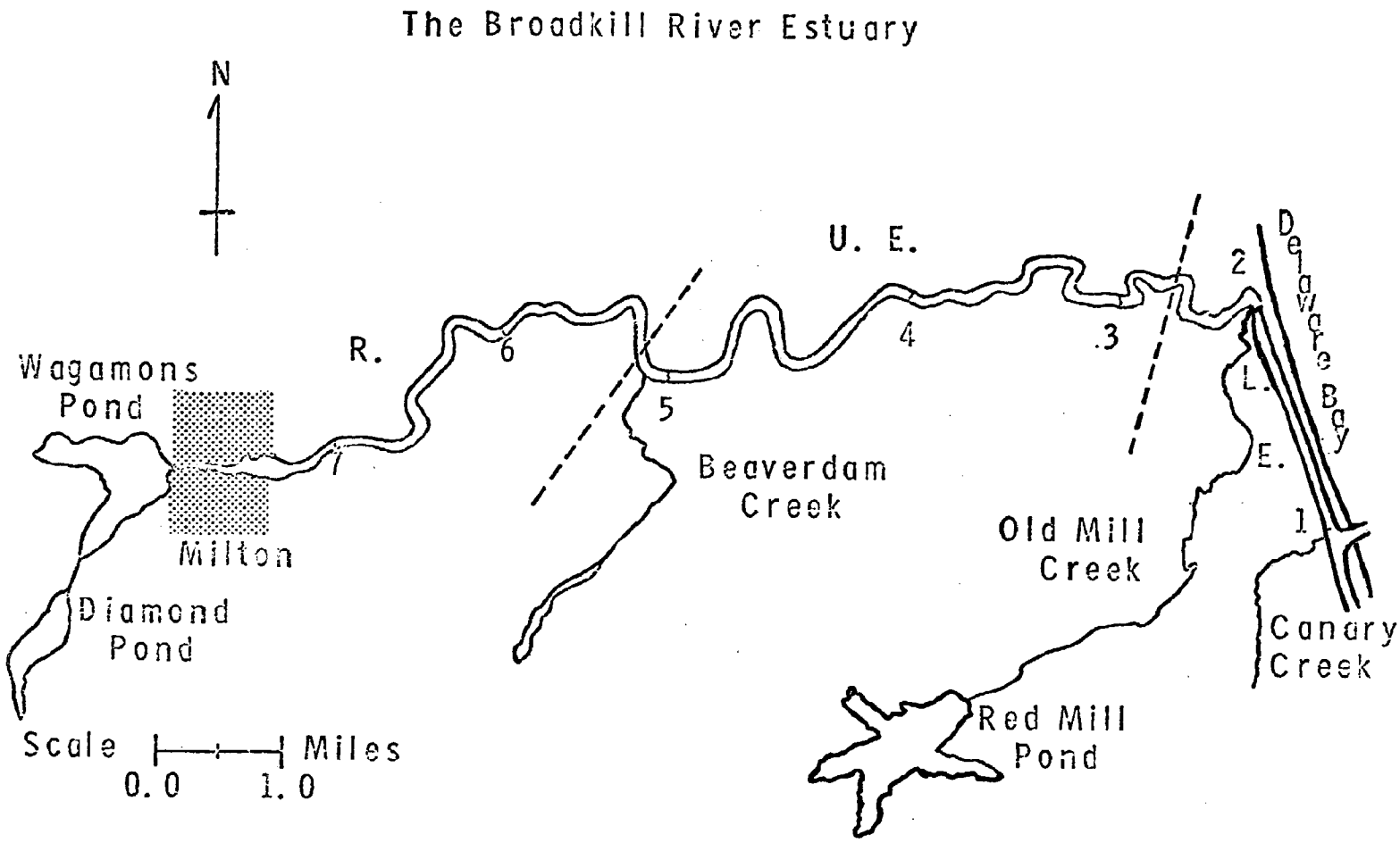

Fig. 1. The Broadkill River Estuarine System: showing the locations of the hydrographic stations and the sections of the system.

L. E. = Lower Estuary
U. E. = Upper Estuary
R. = River

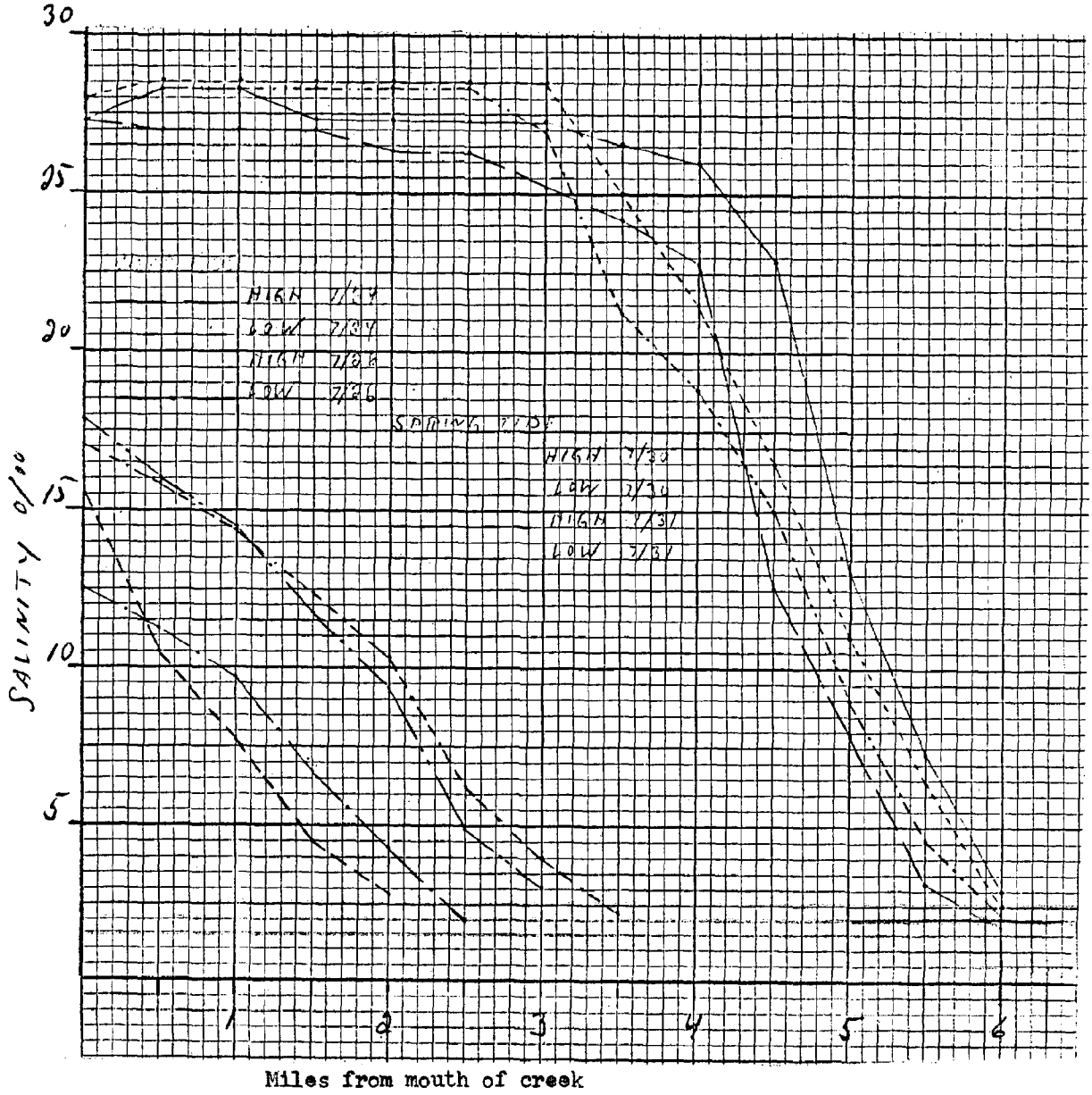

Fig. 2. Slack water salinity distribution in Broadkill Creek on July 24, 26, 30, 31, 1962.

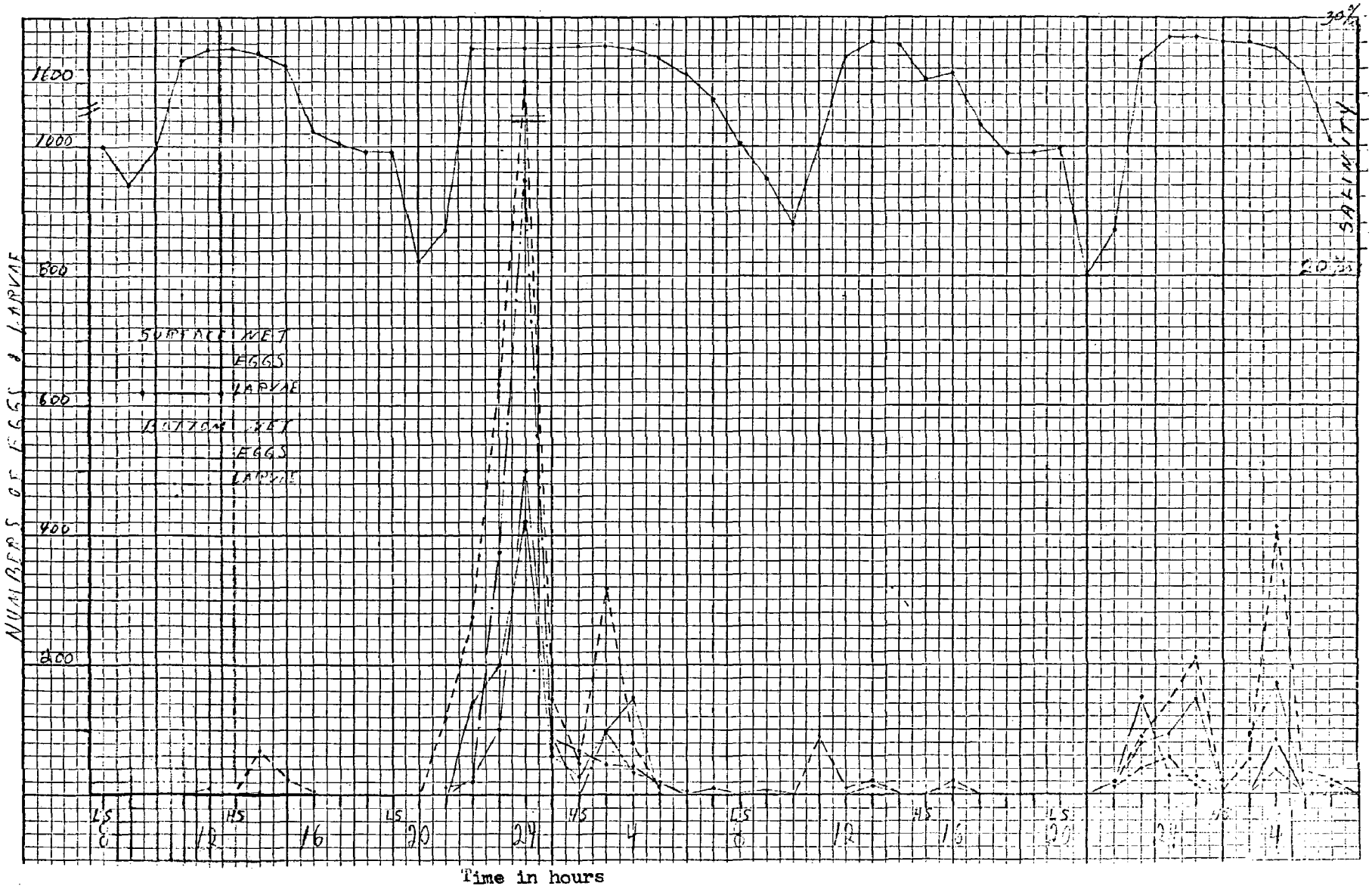

Fig. 3. Numbers of fish eggs and larvae taken from Canary Creek June 6-8, 1962 over a 48 hour period.

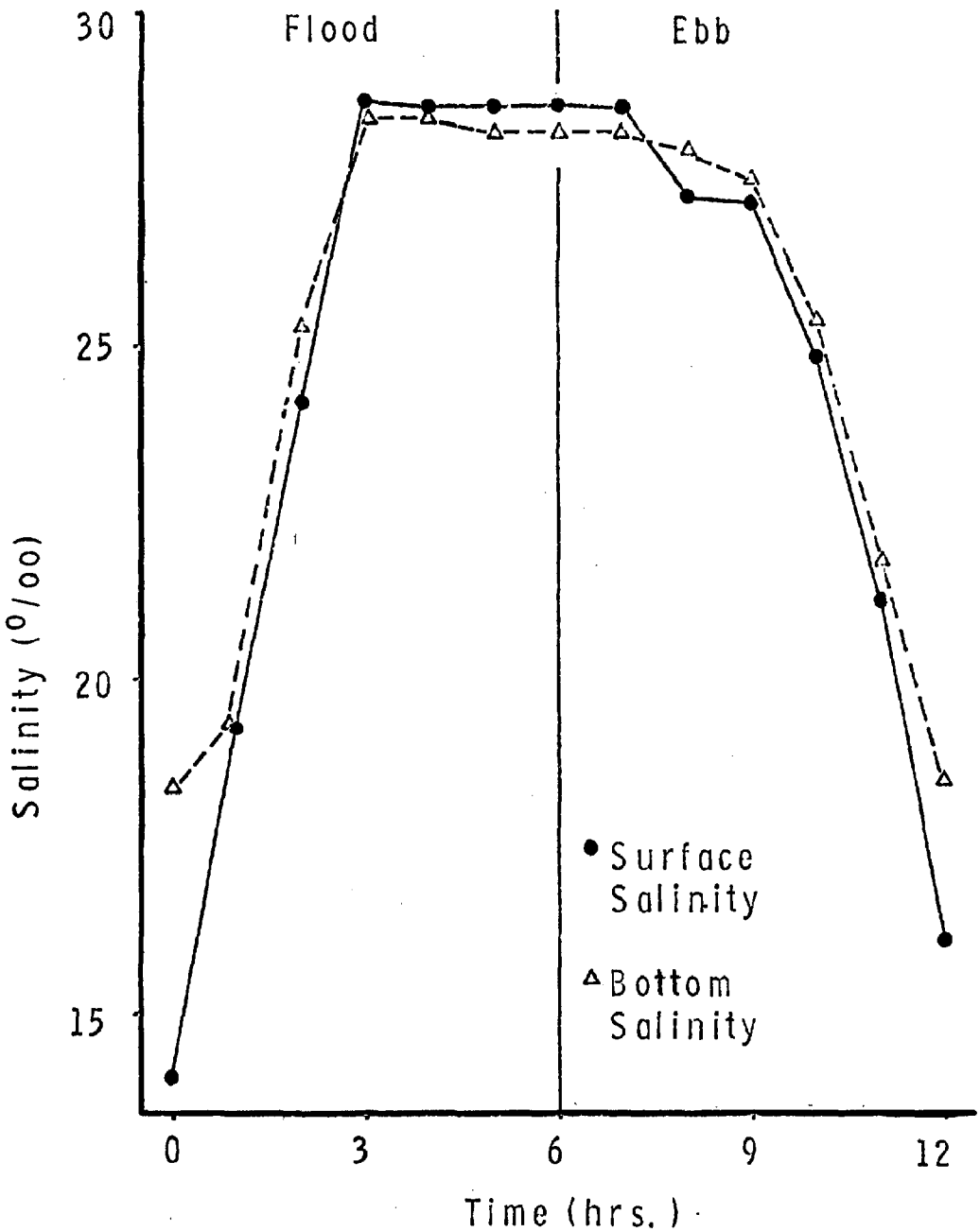

Fig. 4. Variation of surface and bottom salinity over a complete tidal cycle at station 2, July 13, 1967.

HYDROGRAPHY

Wallace de Witt III

The Broadkill River (Fig. 1) is a shallow, positive, coastal plain estuarine system in southeastern Delaware. The hydrography was studied from March, 1967 to January, 1968. Preliminary surveys were conducted on the Murderkill River during the summer of 1967 (de Witt, 1968).

The lower estuarine portion of the Broadkill River (see Fig. 1) was dominated by high salinity water, 33o/oo to 20 o/oo, over most of each tidal cycle. Salinity variations were directly related to the corresponding tidal amplitudes; larger tidal amplitudes produced greater salinity variations. This process operates within the limits imposed by the maximum salinity of Delaware Bay. Seasonal salinity variation did not follow the usual pattern. Heavy rains during the summer reduced the overall salinity of the system while low runoff during the winter produced high salinities. The area appeared to be vertically and laterally homogeneous, except for the presence of a salt wedge at the beginning of each flooding cycle (Fig. 4). The current velocity, 1.65 ft/sec, was the highest mean velocity found in the entire system. Ebbing current velocities were usually stronger than the corresponding flooding velocities. The net movement of water in this area was seaward at all levels. The pH of the water in the area was 7.7, and the mean dissolved oxygen concentration was 6.1 mg-at /l (Fig. 5).

The upper estuarine portion of the system was dominated by a vertically stratified salinity distribution. The salinity varied between 14 o/oo and 1 o/oo over the tidal cycles monitored. The mean current velocity was 1.10 ft/sec, with ebbing currents dominating the water column at all depths.

The river was the section of the estuarine system in which the salinity variations were not directly related to the tidal flow. Seasonal variations in the mean salinity were observed. The mean current velocity was 0.51 ft/sec. The difference between the mean ebbing and mean flooding current velocities was not significant. The mean pH of the water was 6.2, and the mean dissolved oxygen concentration was 0.2 mg-at/l. The low pH values and low oxygen concentrations in this region appeared to be directly related to each other and to the tidal flow.

The Broadkill River is characterized by the presence of three distinct regions of salinity distribution (Fig. 6), one of the characteristics for classifying it as a positive coastal plain estuarine system. The distribution of current velocities with a significant decrease in the mean velocities with distance upstream characterizes the Broadkill River with the shallow bar-built estuaries (Fig. 7).

Data from the Broadkill River indicates a relationship between mean current velocities and discharge, and tidal amplitude, with reservations. This relationship exists during periods of steady runoff and no atmospheric disturbances. Increased runoff and total mixing appear to be directly related to strong current velocities in the lower estuary. The stratified water column and the lower volume of fresh water runoff directed into the

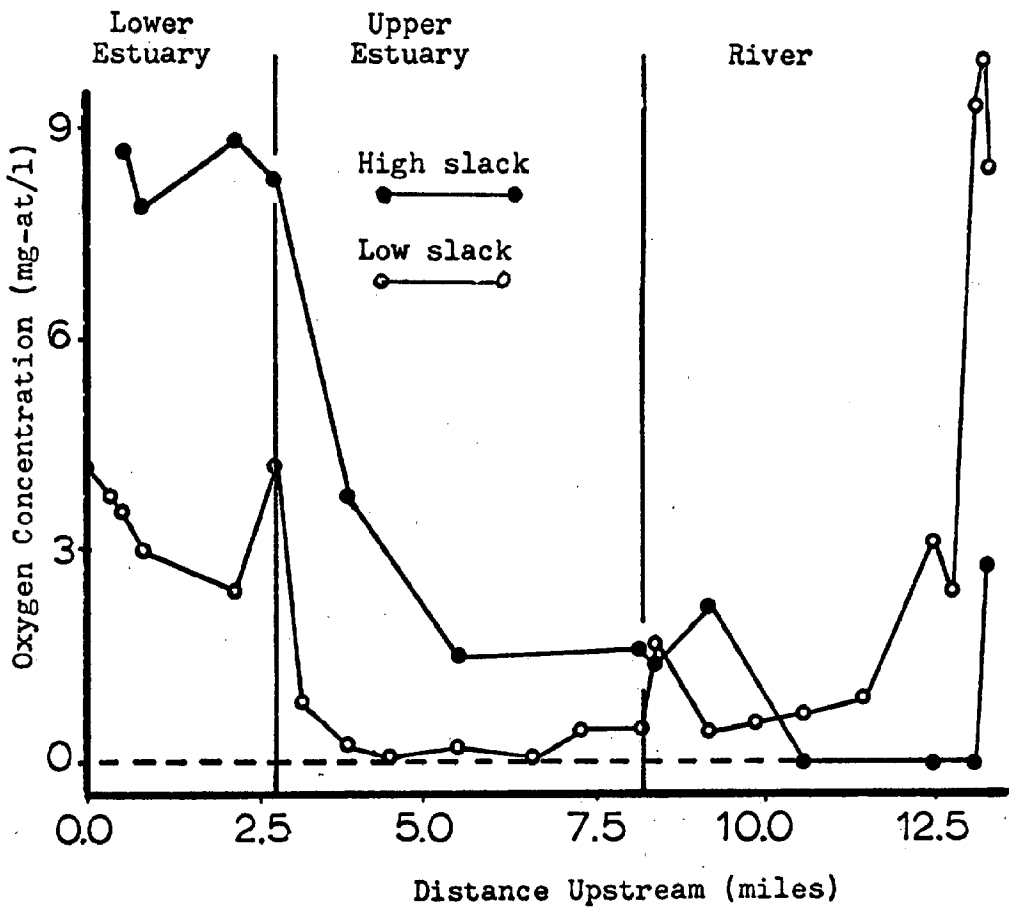

Fig. 5. Variation of the dissolved oxygen concentration over the course of the estuarine system at high slack water, August 8, 1967 and low slack water, July 17, 1967.

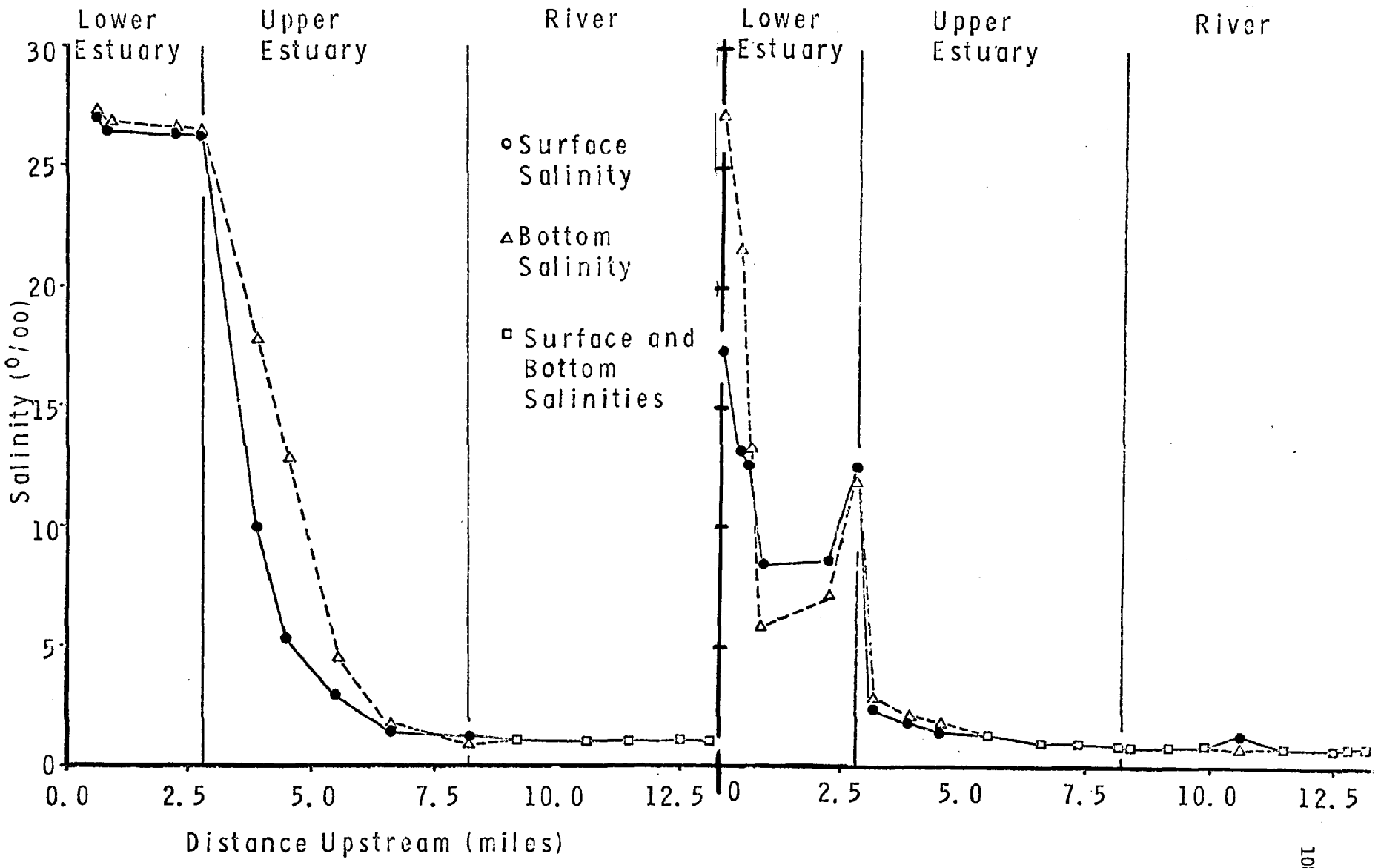

Fig. 6. High slack water, August 8, 1967 Low slack water, July 17, 1967

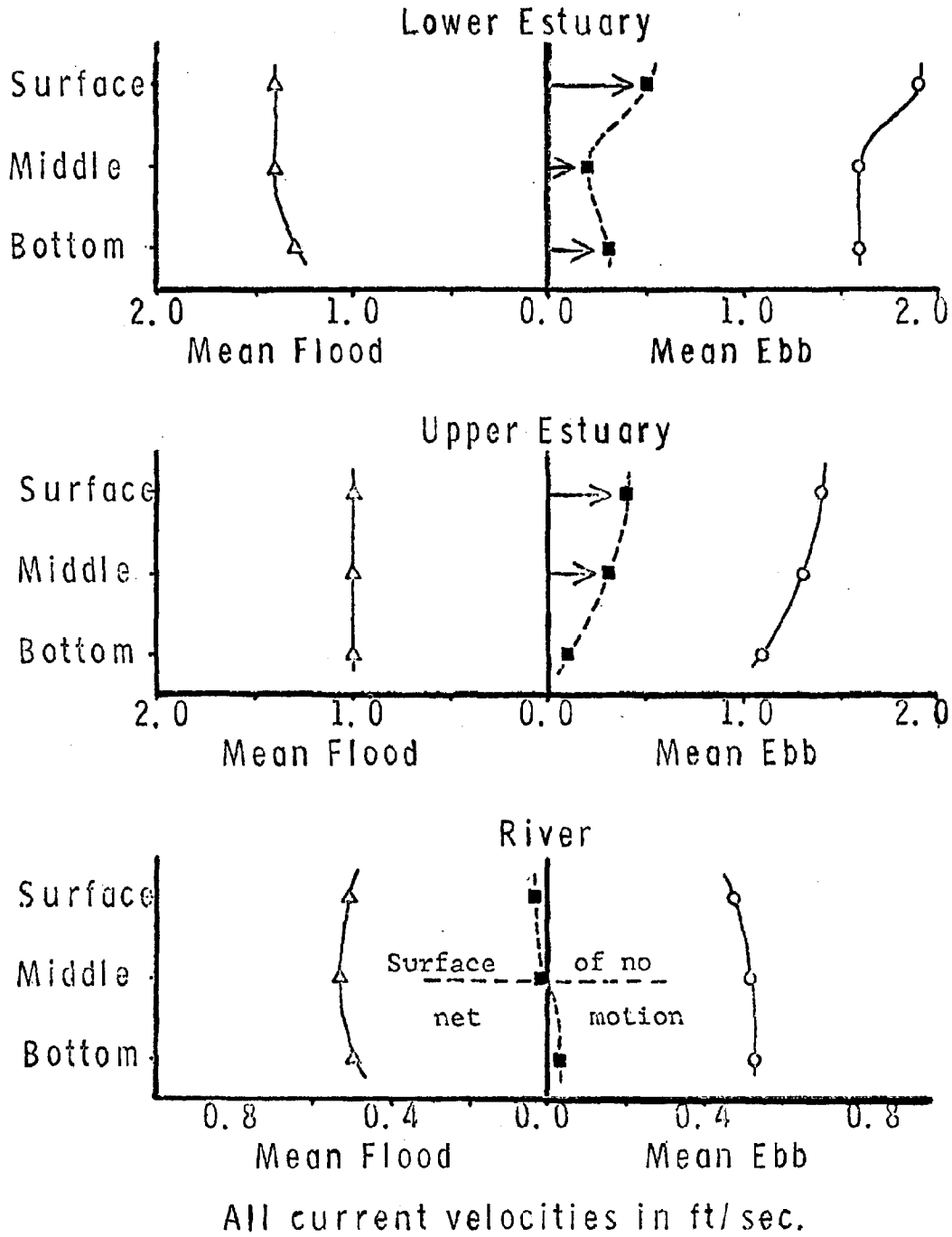

Fig. 7. Mean flooding and ebbing current velocities and the resulting directions and velocities of the net current flow at the most commonly monitored depths in all three regions of the Broadkill River estuarine system.

△ Mean flooding velocities
○ Mean ebbing velocities
■ Mean velocities of net flow

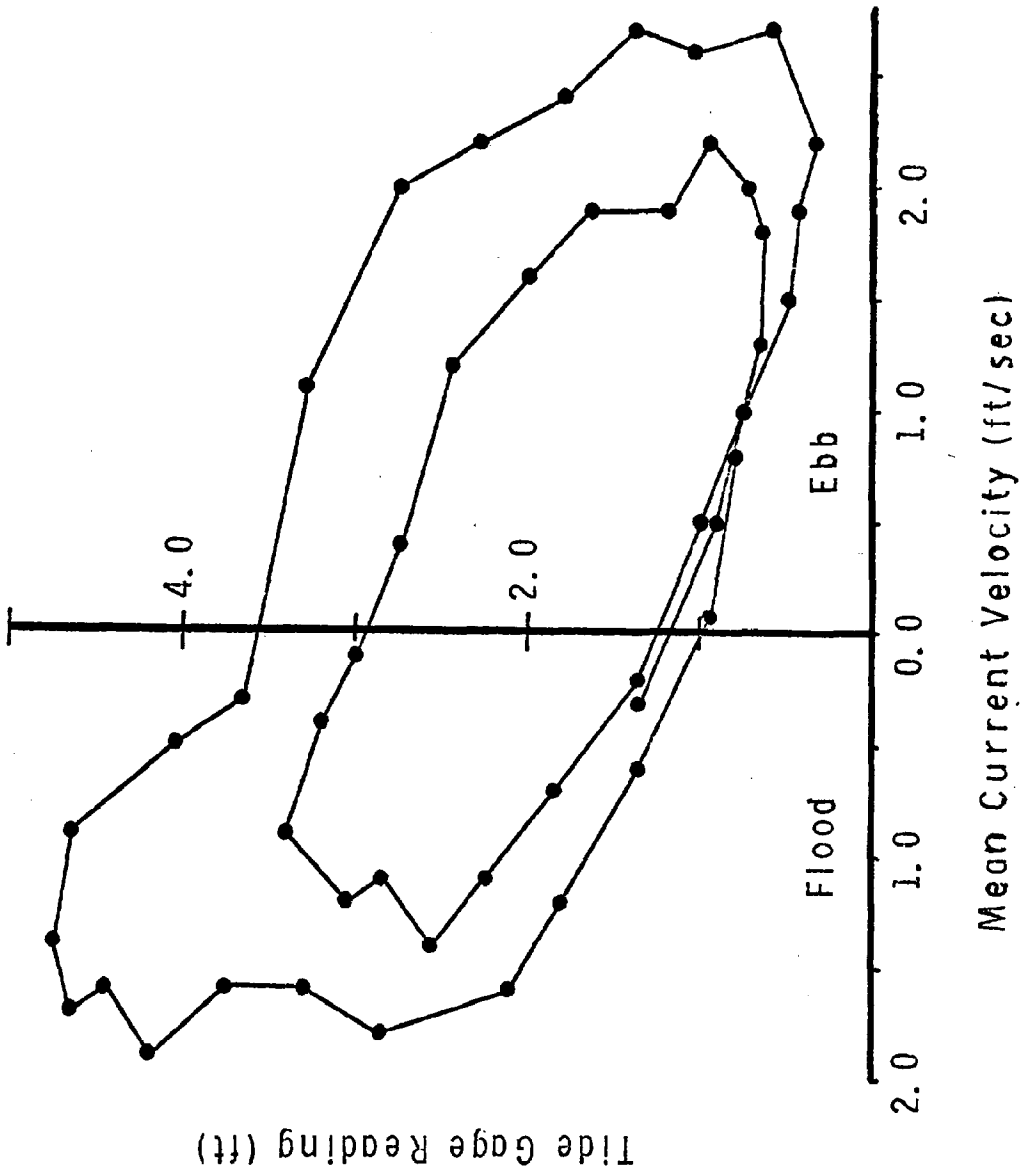

Fig. 8. Variation of mean current velocity with tidal amplitude over two complete tidal cycles at station 1, November 7-8, 1967.

upper estuary appear to be factors controlling its current velocity distribution. However, the differences between the two estuarine sections cannot be based solely upon factors of mixing and discharge. The differences in the origin and configuration of the two channels may play an important part in their current velocity distributions.

The curves for mean current velocity vs. tidal amplitude reflect a change in the character of the tidal wave as it moves upstream (Fig. 8). The inclined elliptical curve of the lower estuary is interpreted as an indication of the presence of oceanic tide-producing forces in a progressive wave form. It is characterized by the change in the direction of the tidal amplitude before the corresponding change in the direction of the current flow. It appears that this wave form is altered as it moves upstream. The wave approaches the standing wave form in the uppermost reaches of the estuary (river) with the highest mean current velocities occurring near the middle of the tidal variation.

The shallow nature of the Broadkill River appears to have a profound effect upon the circulation within the system. The net flow is directed seaward at all levels in the lower and middle reaches of the estuary. Only in the upper portion is there a net upstream flow and it appears in the upper layer while the seaward moving layer occurs along the bottom of the channel. The data indicate an average net volume of fresh water discharge seaward on each tidal cycle of 6 million cubic feet. The data also indicate the system gains fresh water with distance downstream from its head. An estimated 1.5 million cubic feet flows through the entire system from Wagamons Pond. The remainder of the fresh water appears to come from the marshes and creeks drained by the Broadkill River.

Preliminary hydrographic surveys on the Murderkill River were conducted during the summer of 1967. The salinity at the station 4.4 miles from the mouth of the river varied between 25.7 and 0.7 o/oo over the tidal cycles monitored. The mean surface salinity was 14.1 $\pm$ 7.6 o/oo and the mean bottom salinity was 16.2 $\pm$ 8.3 o/oo. The salt wedge was not pronounced, and the water column was well mixed over most of each tidal cycle. The effect of the heavy rainfall during various periods of the summer of 1967 is pronounced (Fig. 9). The mean salinity on August 16 was 2.1 $\pm$ 1.6 o/oo. The mean fresh water percentage on July 19 was 48.4% with a range between 88.3% and 0.1%. On August 16 this mean percentage rose to 95.8%, with a range between 97.4% and 79.6%. Current velocity date indicated that the ebbing currents dominate much of the water column. The mean ebbing current velocity was 1.76 $\pm$ 0.5 ft/sec, while the mean flooding velocity was 1.62 $\pm$ 0.7 ft/sec. Both mean current velocities appeared to reach their maximum strength in the mid-depth region. The mean current velocity vs. tide gage height produced an inclined elliptical curve which indicates the area is dominated by semi-diurnal oceanic tide-producing forces.

The mean dissolved oxygen concentration over the tidal cycles monitored was 4.25 mg-at/l with a range between 2.42 and 7.00 mg-at/l. The oxygen concentration appeared to reach a peak near the end of the flooding cycle and to decline throughout the ebb tide.

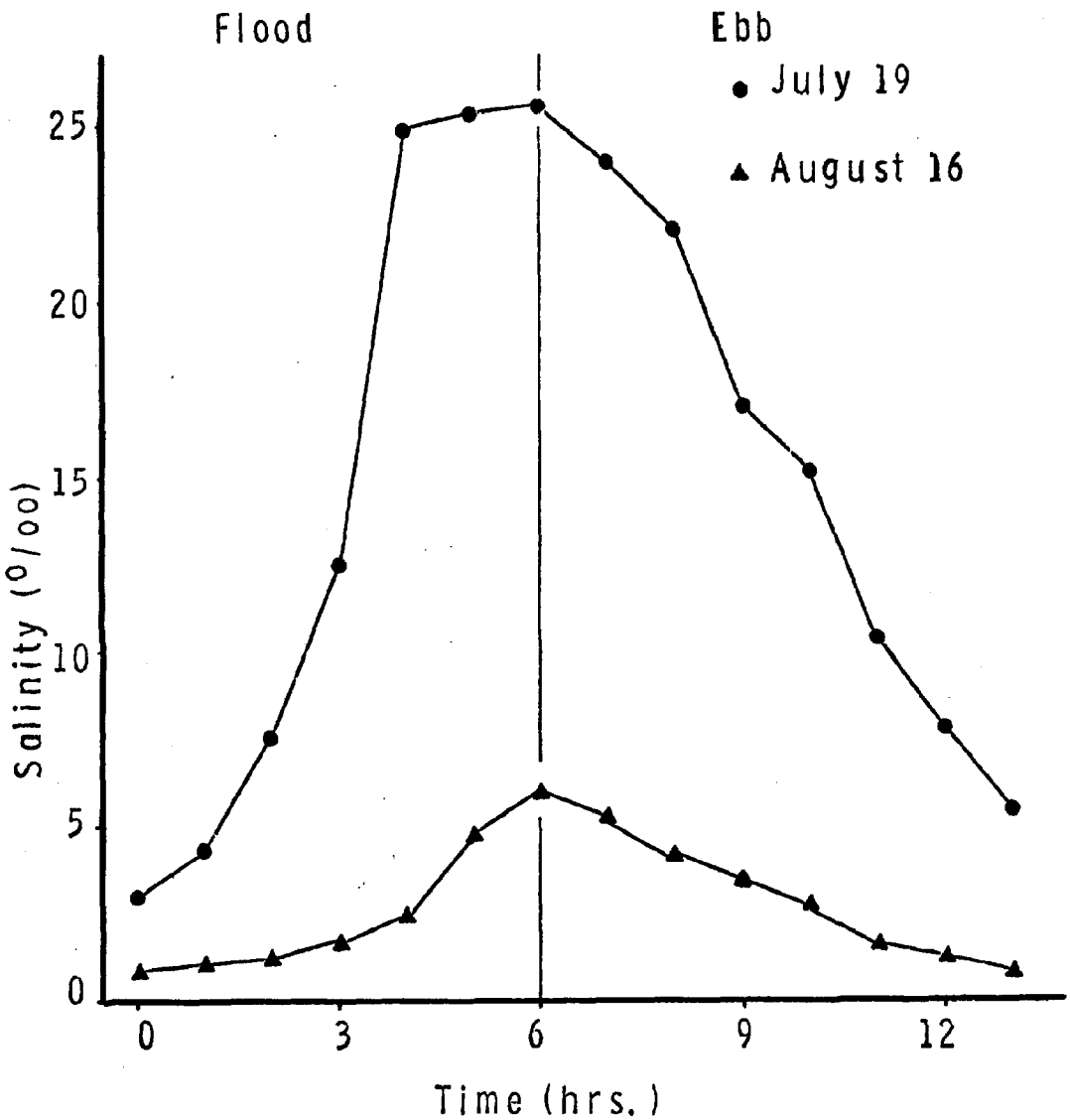

Fig. 9. Comparison of the variation in mean salinity of the Murderkill River over a complete tidal cycle on July 19 and August 16, 1967.

BIOGEOCHEMICAL CYCLES

Evidence for Dissolved Phosphorus Hypereutrophication

Robert J. Reimold

The effects of marshland manipulation by man have received little attention concerning their influence on the biogeochemical cycles of the salt marsh. The seasonal fluctuations of nutrients such as phosphorus have also received little attention when considering the salt marsh ecosystem. The literature suggests that nutrient cycles are atypical when compared to the nutrient fluctuations in the oceans. The purpose of this study was to evaluate the periodicity of dissolved phosphorus concentrations in the salt marsh and also to evaluate various types of marshland management and their effects on the phosphorus concentrations.

For this study, total, inorganic, and organic dissolved phosphorus concentrations were measured at monthly intervals from seven different types of marshland common in the State of Delaware. Related physical parameters were evaluated concurrently with the phosphorus samples. Sampling procedures were carried out at six hour intervals over one twenty-four hour period during each monthly collection. All data were analyzed statistically with the aid of a computer to reveal statistically significant relationships.

The results (Table 3) indicate that phosphorus concentrations of the salt marsh areas investigated were considerably higher than previously reported concentrations for estuarine areas. These higher concentrations of the various forms of phosphorus measured reveal hypereutrophication of the salt marsh waters. There are significant interactions between various physical parameters and phosphorus concentrations. The following discussion is limited to those relationships found to be statistically significant (99.5% confidence interval). The concentrations of the various forms of dissolved phosphorus are related to salinity levels in the tidal creeks, and natural and ditched marshes. This salinity-phosphorus relationship is an indication of increasing phosphorus concentrations with decreasing salinity; this information associated with a significant volume of fresh water to the bay on each ebb tide (de Witt, 1968), indicates a net transport of phosphorus from the marsh to the bay. There is a significant relationship between tidal stage and phosphorus concentrations, lending further support to the supposition that the marsh makes significant phosphorus contributions to the bay. There are seasonal fluctuations in the abundance of the three forms of phosphorus with values increasing until the middle of the year and decreasing to a minimum during the winter months (Figs. 10 and 11).

Concerning the effects of marshland manipulation, the highest concentrations were found in the natural marsh area (Table 3). The natural marsh was significantly different from all other types of managed marsh area studies in relation to the phosphorus concentrations. There did not appear to be a difference between a new and an old champagne pool. The effects of

Table 3. Mean values of various measured parameters from various types of managed salt marshes in Delaware.

Parameter	Ditched Marsh	Tidal Creek	High Level Imp.	Low Level Imp.	New Champ. Pool	Old Champ. Pool.	Natural Marsh
Total P ug-at/l	19.2	8.6	13.4	16.5	13.2	13.2	25.8
Inorg. P ug-at/l	11.4	4.9	7.2	8.4	6.1	5.3	18.0
Org. P ug-at/l	8.7	3.7	6.2	8.1	7.1	7.9	7.7
Salinity o/oo	25.1	24.7	2.7	13.3	13.6	17.7	11.9
pH	7.3	7.3	6.6	7.3	7.4	7.4	6.9
Water Temp.	16.3	16.4	16.0	15.7	15.8	16.0	15.0
Air Temp.	17.4	17.0	14.8	14.6	14.8	14.8	14.6

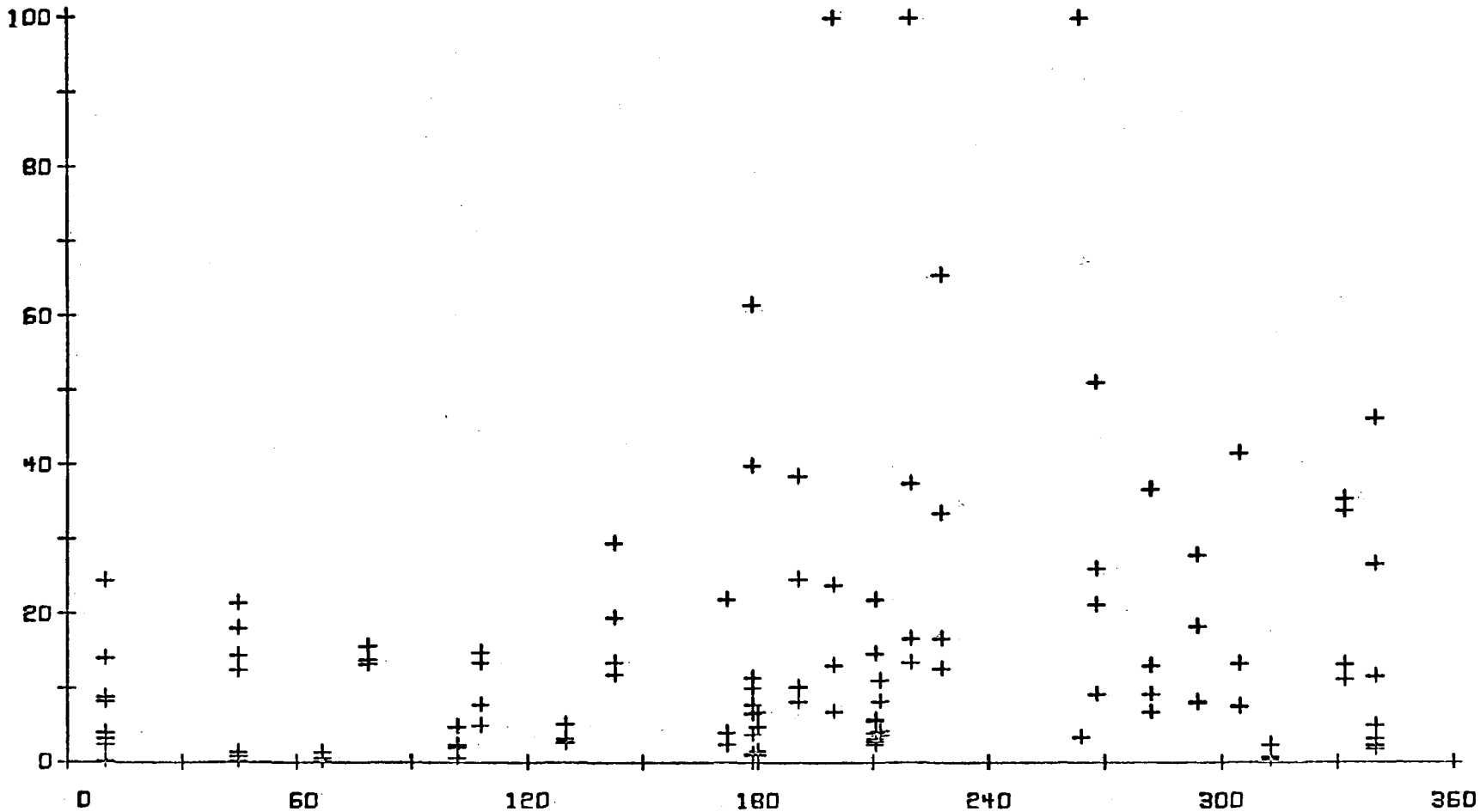

Fig. 10. Inorganic phosphorus concentrations vs. day of year representing data collected from Station 29, natural marsh. Abcissa = day of year; Ordinate = inorganic dissolved phosphorus concentration, ug-at/l.

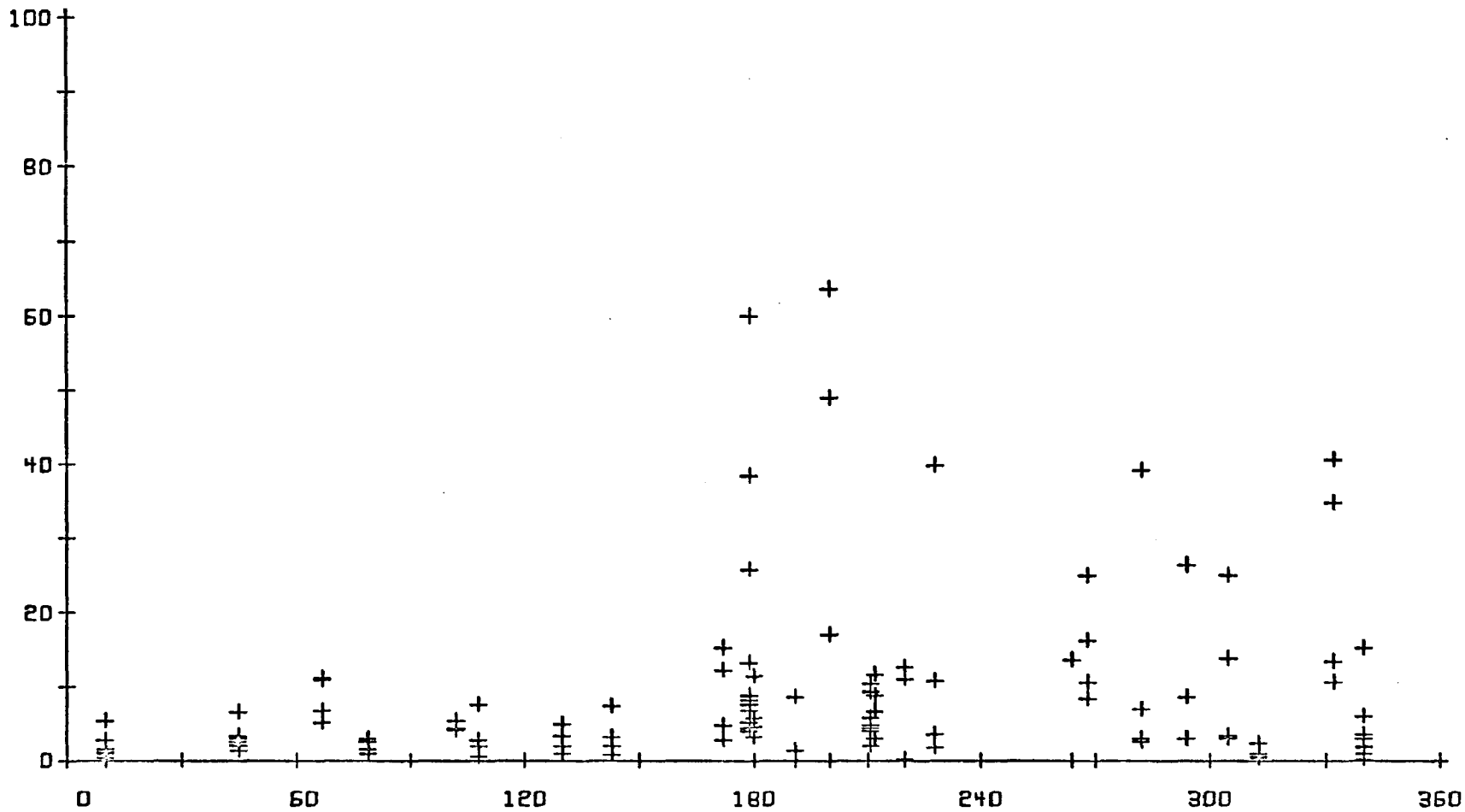

Fig. 11. Organic phosphorus concentrations vs. day of year representing data collected from Station 29, natural marsh. Abcissa = day of year; Ordinate = organic dissolved phosphorus concentration, ug-at/l.

the high level impoundment, low level impoundment and champagne pools were similar in that they all tended to depress the concentrations of phosphorus when compared to a natural marsh area. The data suggest that the best type of marshland management with respect to phosphorus concentrations, is no management practice at all. Of the management practices considered, the ditched marsh areas are significantly lower in phosphorus concentration than the natural marsh, however the ditched areas represent the least alteration, of the various management procedures considered.

Fractionation of Inorganic Phosphorus from Canary Creek Soils

Maureen A. Gorman

Tidal marsh muds were analyzed for aluminum, reductant soluble iron, calcium and iron phosphates. No traces were found of the first two. Calcium and iron phosphate concentrations increased with soil depth (Table 4). As a result of weathering there was a decrease in the amount of inorganic phosphate in marsh soil; sandy soils the lowest, organic soils intermediate, and silt-clay soils the highest (Table 5). Calcium phosphate was always higher than iron phosphate in all samples processed.

Hydrogen Sulfide Production and Its Effect on Inorganic Phosphate Release from the Sediments of the Canary Creek Marsh

Emmy Lou Gooch

The seasonal variation of hydrogen sulfide production in the Canary Creek marsh has been measured over the period of one year. It was found that the greatest production occurred during the late spring months (Fig. 12) and the least production occurred during the winter months. This seasonal production would seem to be strongly related to seasonal temperature changes within the sediments and to the seasonal variation of salinity and the concentration of sulfate in the water. Hydrogen sulfide release from the sediment appears to be a function of the pH and the concentration of dissolved iron in the waters. In general, the higher the iron concentration, the less hydrogen sulfide is released (Fig. 13).

The anaerobic microorganisms responsible for sulfide production were identified as members of two genera, and their location was related to the sediment environment in which they were found. It was ascertained that the genus Desulfotomaculum was found in the environment which repeatedly changes with respect to salinity and sediment moisture; whereas, the genus Desulfovibrio was found in the more constant environment. The physical state of the waters trapped within the marsh sediments established a ratio of 5:3 of gravity to bound water in the predominantly sand sediments, and in the clay sediments these variables were found in a ratio of 3:5.

Statistical analysis indicates that there are no physical or chemical factors which act separately to affect the anaerobic bacterial population density and hydrogen sulfide production.

The concentration of total iron was ascertained in an attempt to elucidate the mechanism by which inorganic phosphate is released from the sediments. It was found that iron and sulfide were present in concentrations of sufficient magnitude to permit pyrite formation.

Table 4. Concentration in ug-at/l of inorganic phosphate in Canary Creek marsh soils.

No. of Samples	Depth Inches	Concentration ug-at/l	
		Fe	Ca
34	surface	0.16	26.3
19	18	0.23	39.1
18	24	0.62	40.0
14	30	4.52	19.4
16	60	6.70	24.7
15	72	18.83	47.7

Table 5. Concentration of inorganic phosphate relative to soil texture (identification of soil texture by visual means).

No. of Samples	Texture	Concentration ug-at/l	
		Fe	Ca
8	sand	.001	--
9	sand	.004	--
12	organic	.020	.09
2	organic	.028	.12
2	clay-silt	.503	52.4
2	clay-silt	7.83	22.9

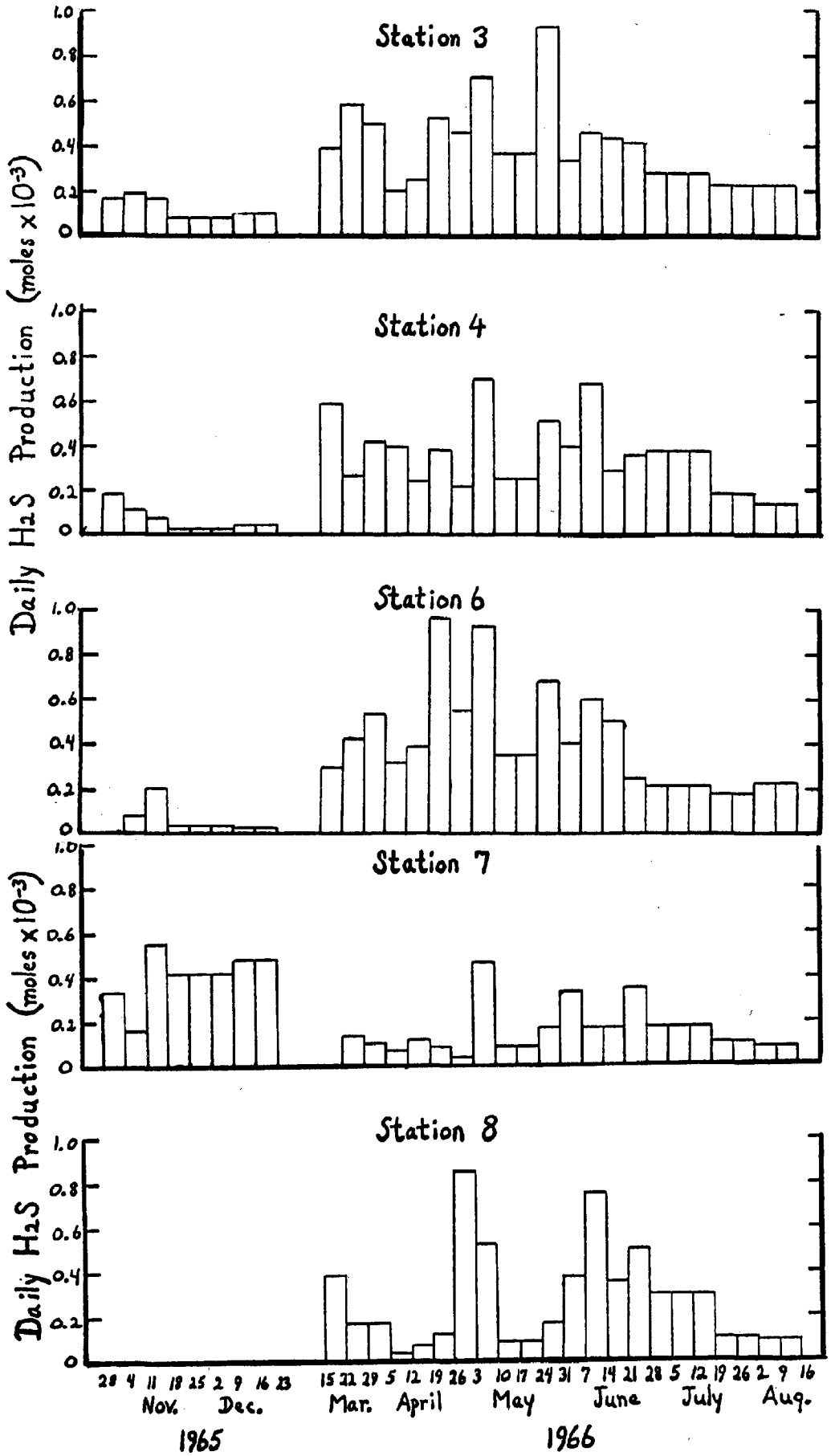

Fig. 12. H_2S production in the Canary Creek marsh.

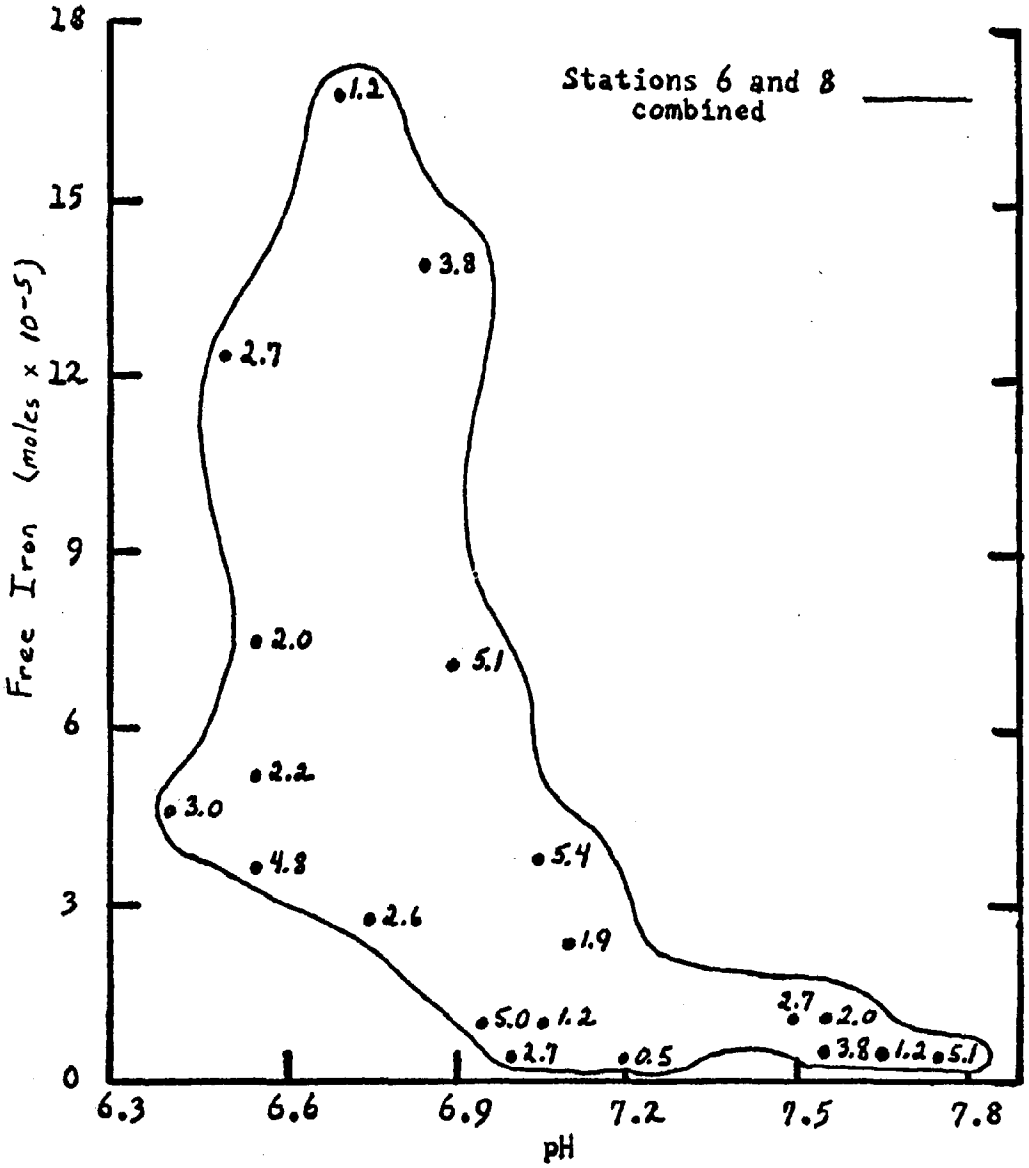

Fig. 13. Weekly release of H_2S (moles x 10^{-3}) as a function of pH and free iron.

A cycle of seasonal binding and release of inorganic phosphate from the sediments in the Canary Creek marsh was postulated (Fig. 14).

The occurrence of soluble iron and sulfide ions in the sediments is the primary cause for the release of inorganic phosphate. There is a complicated relationship between the solubility of iron, the Eh and pH of the sediment, and the products of the sulfur cycle. In general, iron solubility is favored under acid reducing conditions. However, sulfur in the sediments is known to be in part in the form of sulfuric acid and its reduction to sulfide causes the sediments to become more alkaline. The presence of both sulfides and an alkaline condition tend to lower the solubility of iron. A decrease in iron solubility is also caused by a change from the anaerobic to an aerobic condition which results in the oxidation of ferrous iron. Sulfides under aerobic conditions are oxidized with a resulting increase in sediment acidity which in turn favors the increased solubility of iron. Thus, conditions conducive to reduction of sulfates promote reduction of ferric iron, and result in the formation of iron sulfides; and conditions which contribute to the oxidation of sulfides promote the oxidation of ferrous iron and result in the formation of insoluble metal salts of phosphorus. The high water content of the sediments together with the excess amount of organic carbon in the Canary Creek marsh are the primary factors which allow for the presence of the hydrogen sulfide producing bacteria. Once these organisms are established, the factors which regulate the rate and the quantity of sulfide produced are temperature, salinity, and the abundance of sulfates available to them for their metabolism. It is evident that in this marsh the environmental conditions which allow for the production of hydrogen sulfide are present.

The Seasonal and Spatial Distribution of Nitrate and Nitrite in the Surface Waters of Two Delaware Salt Marshes

Don Aurand

The distribution of nitrate and nitrite in two areas of Delaware salt marsh was studied from July, 1966 to December, 1967. The areas studied were: Canary Creek marsh, near Lewes, Delaware at the mouth of Delaware Bay, and the Murderkill marsh, located in central Delaware on the Murderkill River.

The results of this study indicate that at high slack water the Canary Creek marsh is characterized by high salinity, low nitrate water, while the Murderkill marsh is characterized by low salinity, high nitrate water from the Murderkill River. Man-made control structures found in the Murderkill area inhibit free tidal exchange, and result in the lowering of the high slack water nitrate concentration within the impounded area (Tables 6, 7; Figs. 15, 16, 18, 19, 21, 22).

In both marshes (Figs. 16, 19, 22) seasonal variations in nitrate were observed, with maximum values in the winter and minimum values in the summer. The nitrate concentrations at Canary Creek ranged from nearly zero in the summer to about 30 ug-at/l in the winter. In the Murderkill marsh nitrate concentrations in the winter were in the range 40-100 ug-at/l and decreased to approximately 10 ug-at/l in the summer. Fresh water runoff is assumed to be the source of the high nitrate concentrations in the Murderkill River.

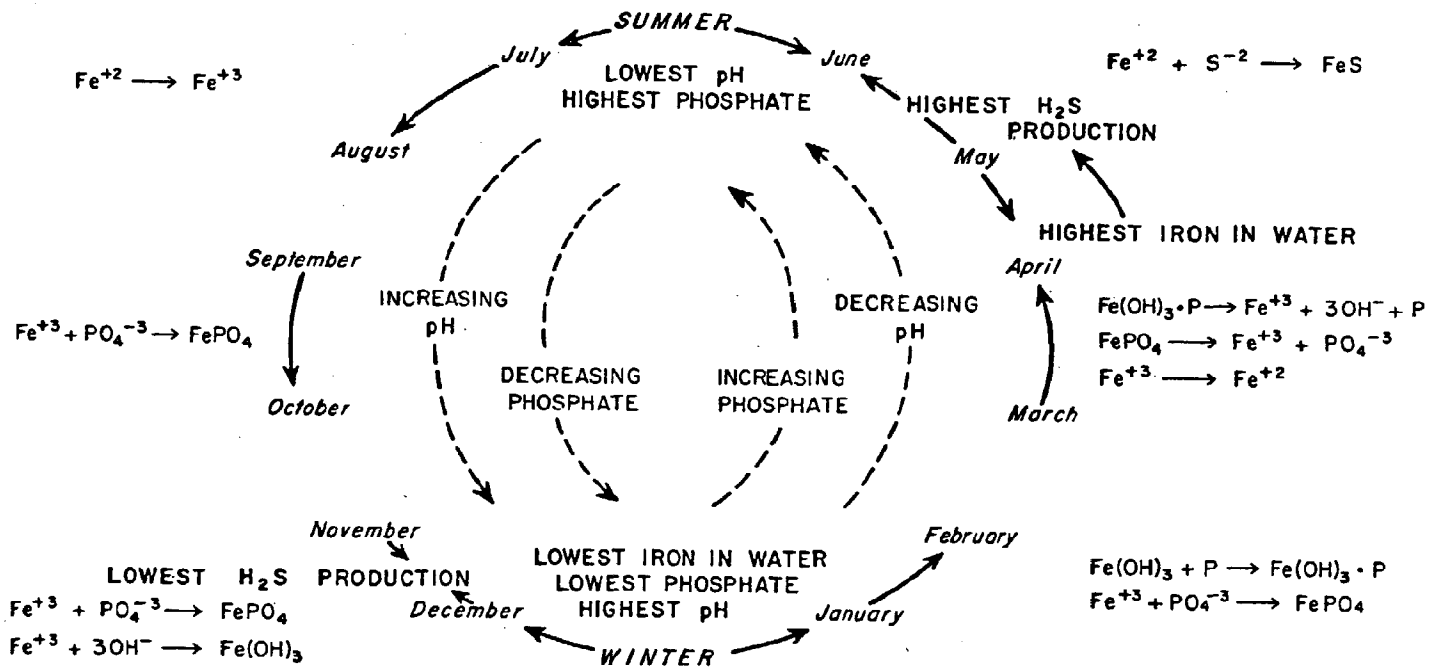

Fig. 14. Chemical processes in Canary Creek marsh which cause the release of inorganic phosphates.

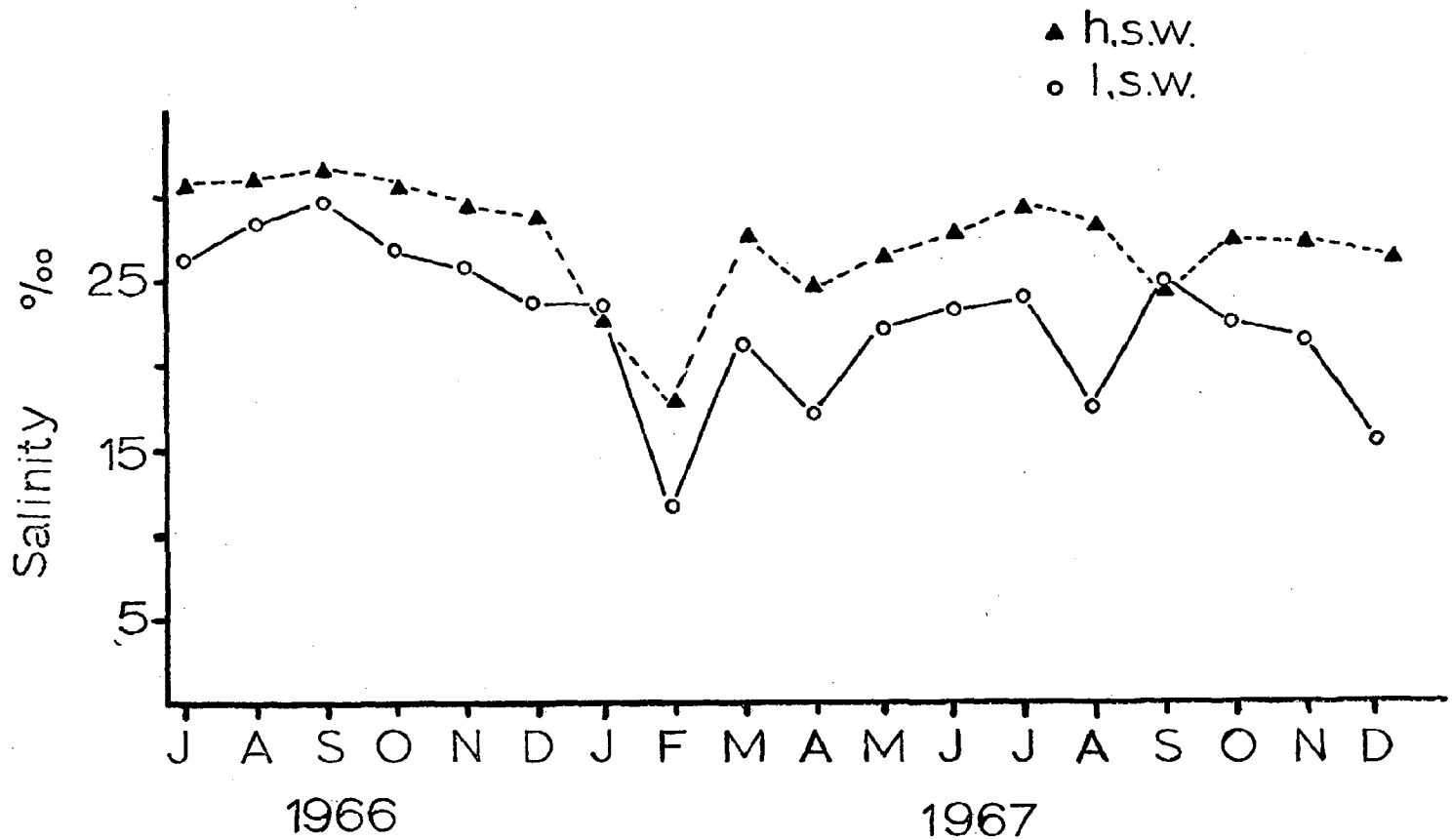

Fig. 15. The seasonal variation in salinity at Canary Creek. All values are monthly averages (h.s.w. - high slack water, l.s.w. - low slack water).

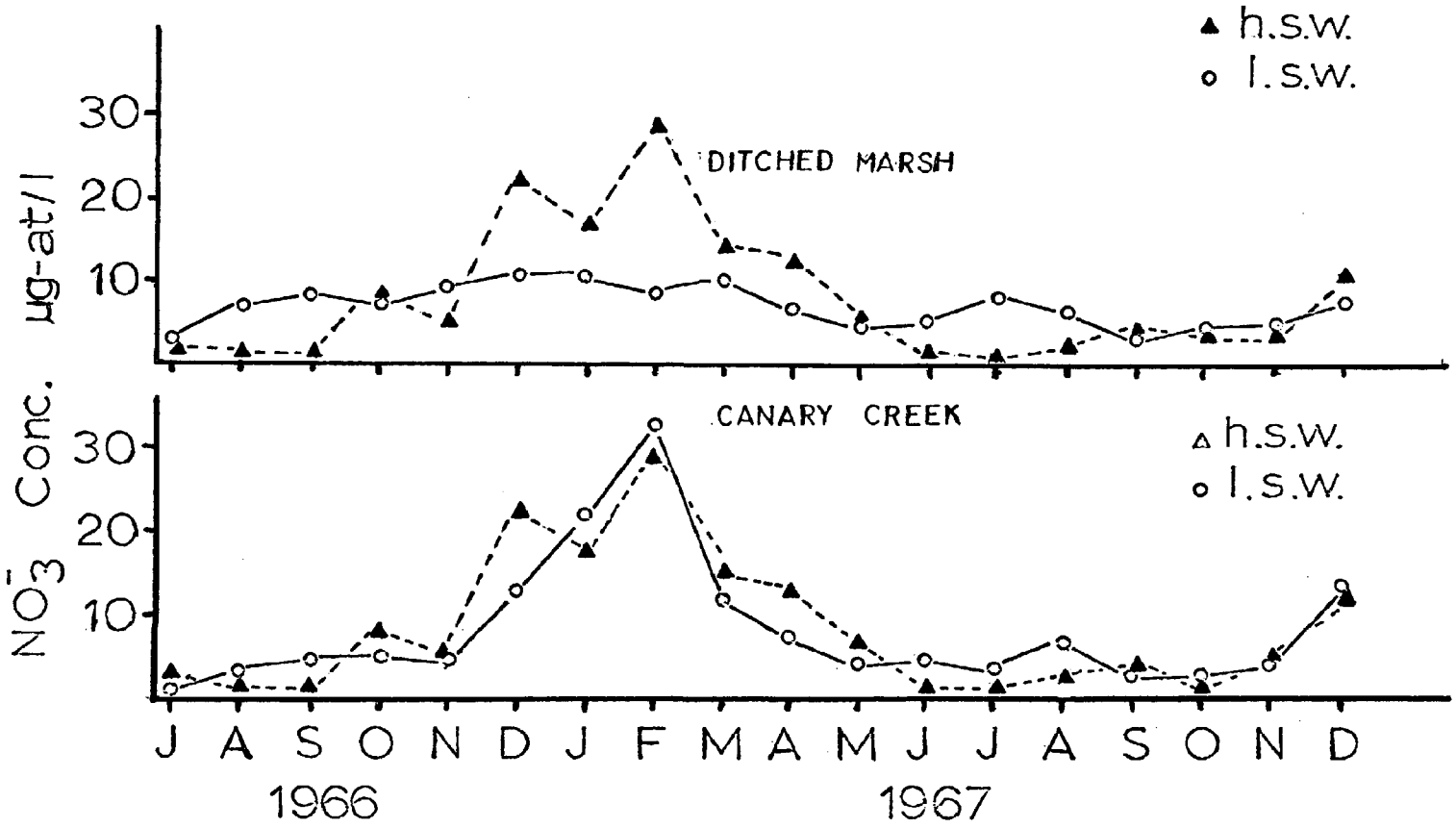

Fig. 16. The seasonal variation in nitrate observed in Canary Creek marsh. All values are monthly averages (h.s.w. - high slack water, l.s.w. - low slack water).

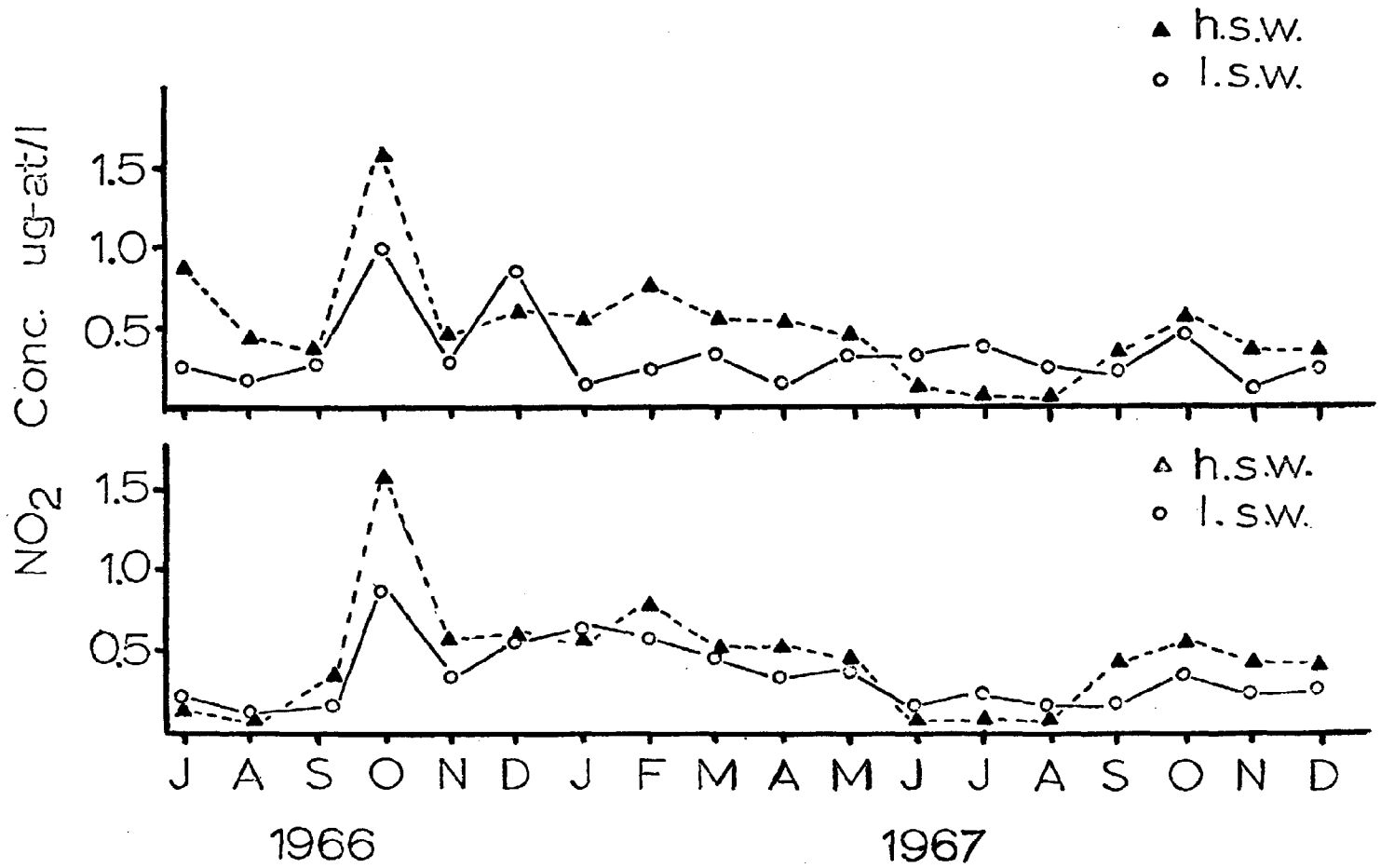

Fig. 17.- The seasonal variation in nitrite concentration observed in Canary Creek marsh. All values are monthly averages (h.s.w. - high slack water, l.s.w. - low slack water).

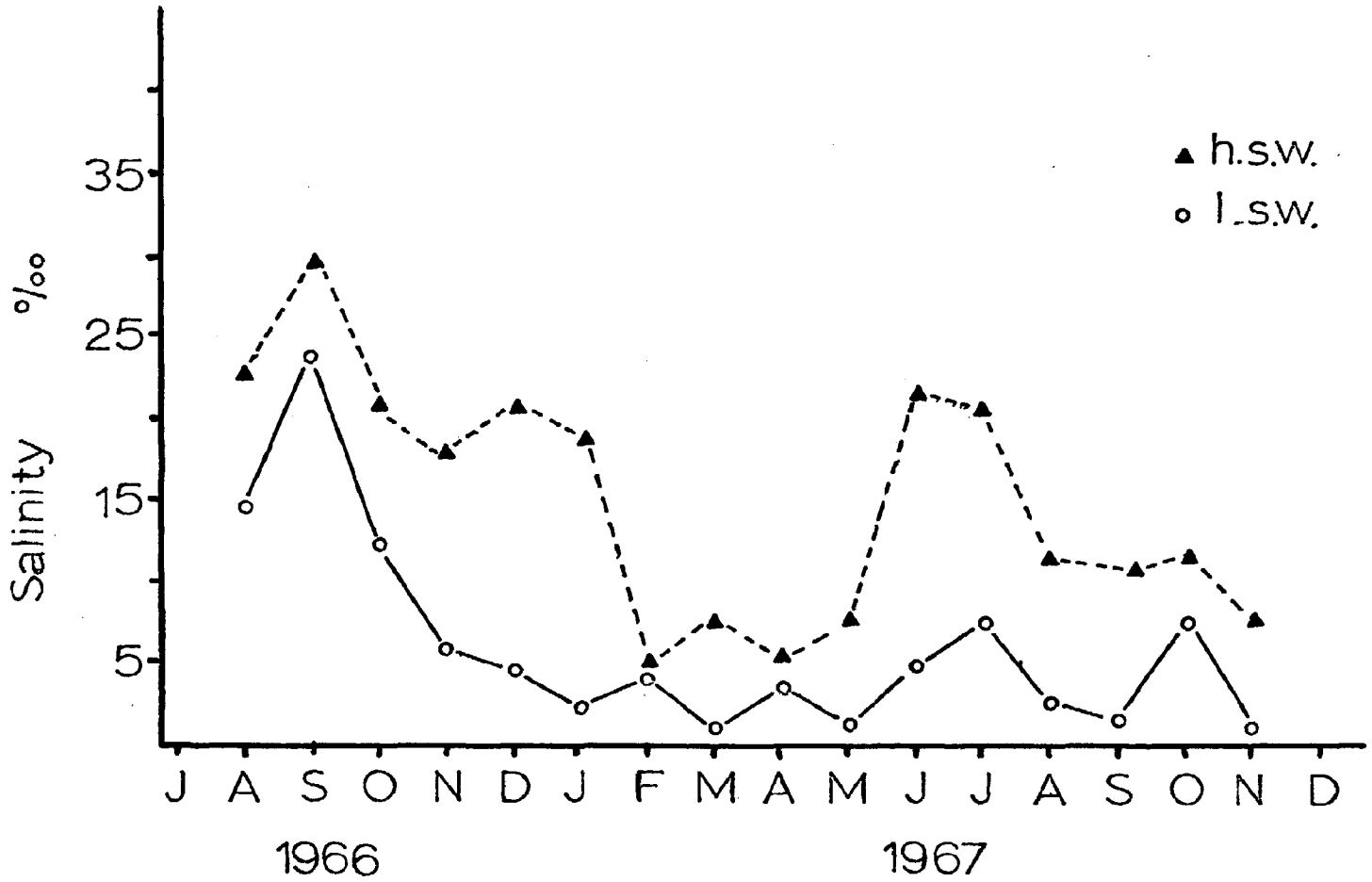

Fig. 18. The seasonal variation in salinity in the Murderkill River. All values are monthly averages (h.s.w. - high slack water, l.s.w. - low slack water).

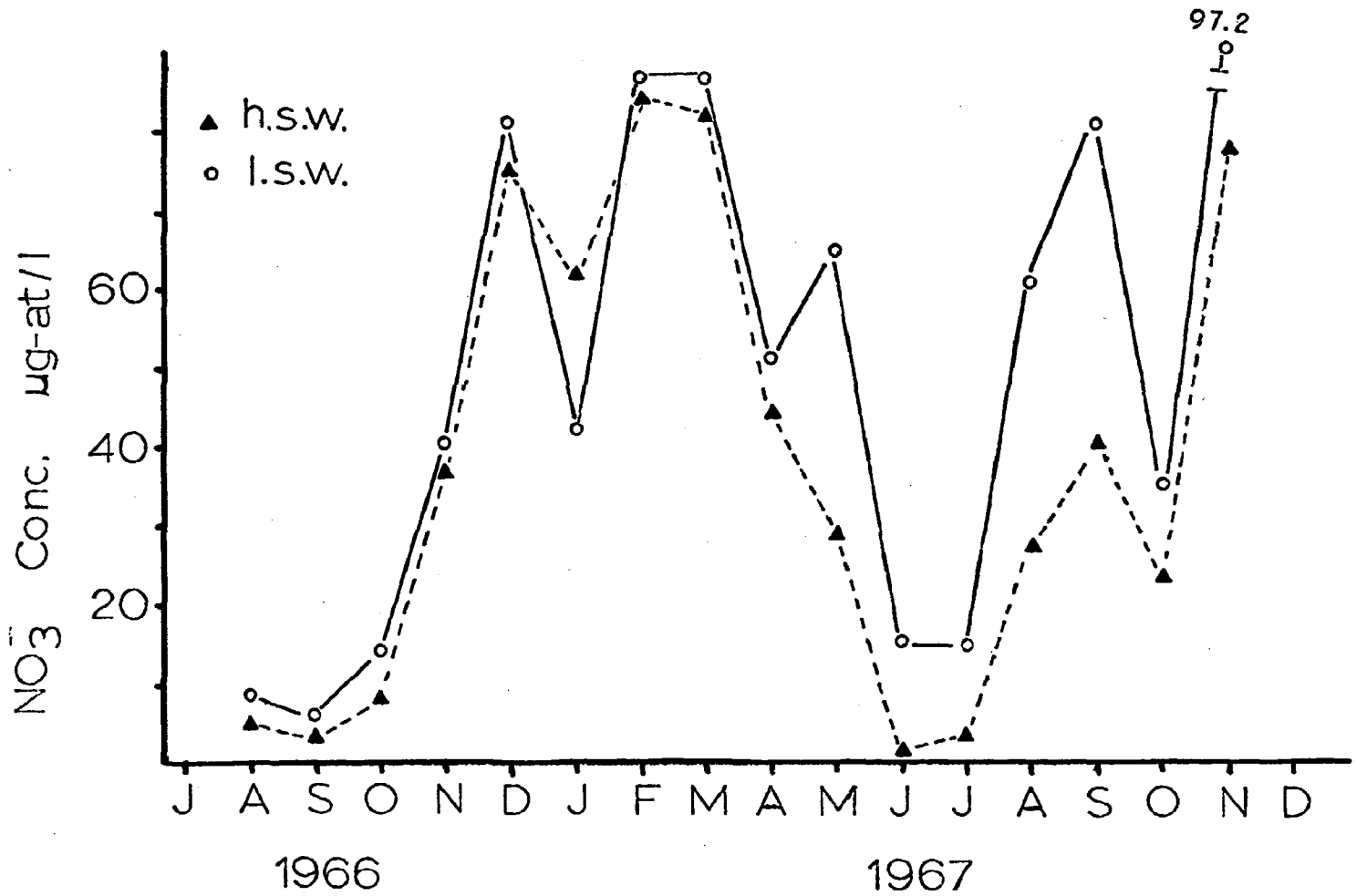

Fig. 19. The seasonal variation in nitrate concentration in the Murderkill River. All values are monthly averages (h.s.w. - high slack water, l.s.w. - low slack water).

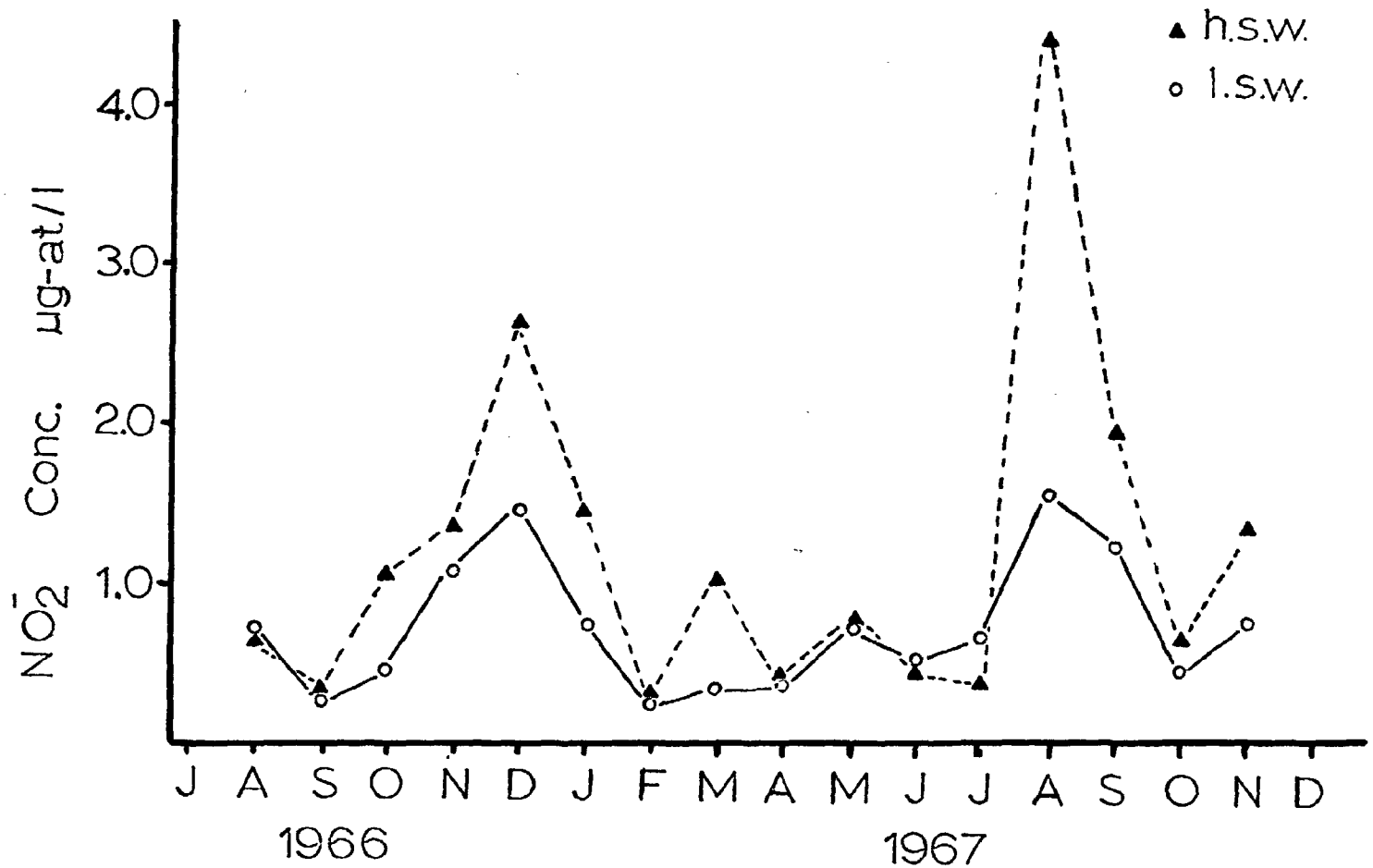

Fig. 20. The seasonal variation in the nitrite in the Murderkill River. All values are monthly averages (h.s.w. - high slack water, l.s.w. - low slack water).

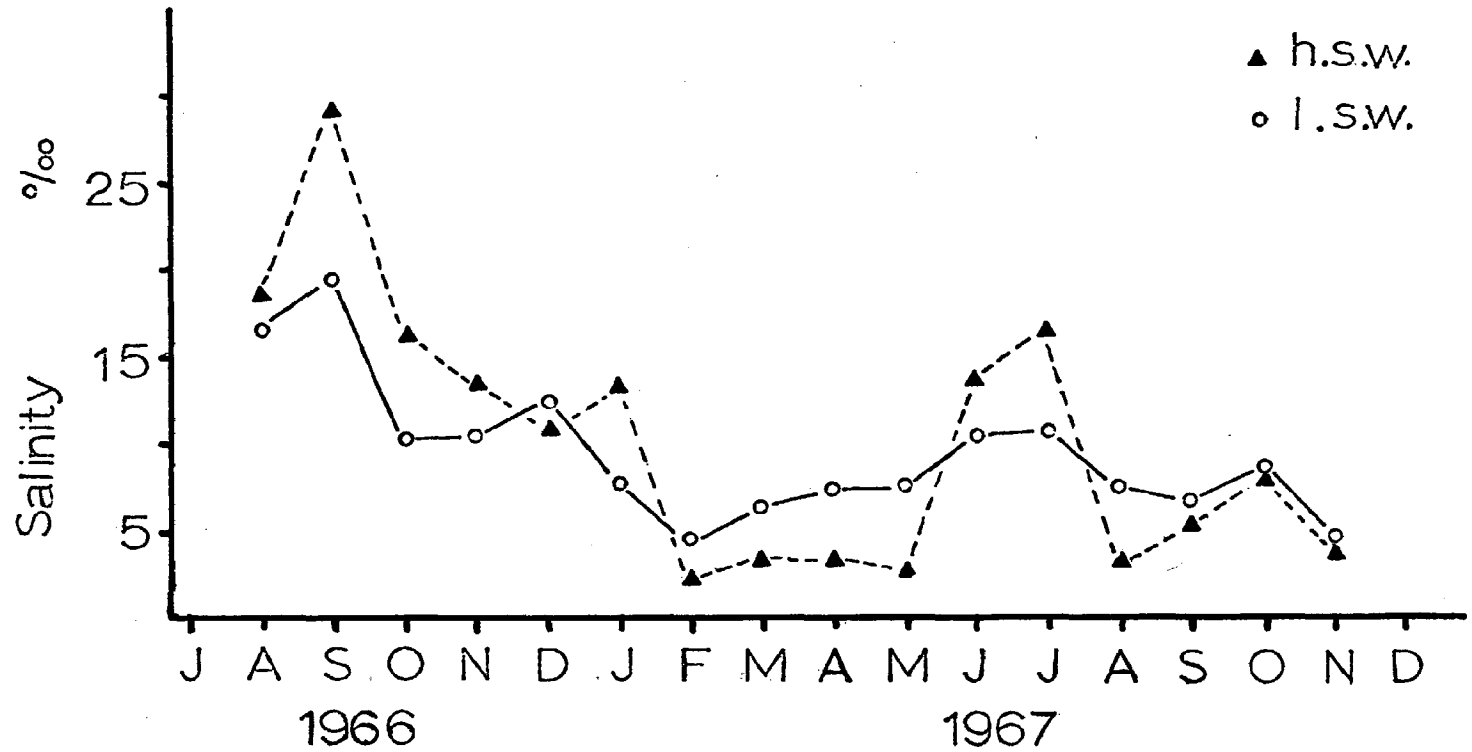

Fig. 21. The seasonal variation in salinity in the natural marsh. All values are monthly averages (h.s.w. - high slack water, l.s.w. - low slack water).

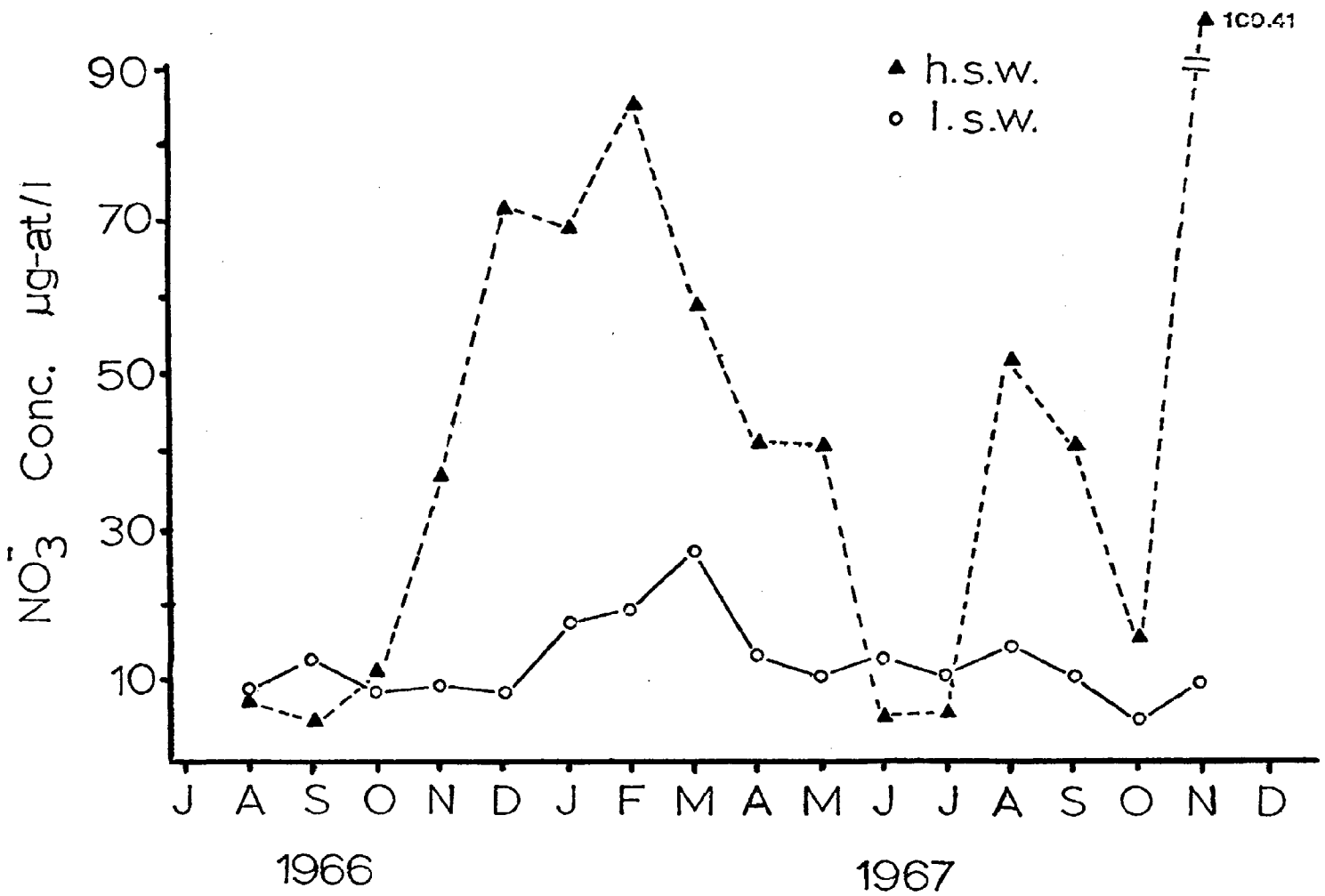

Fig. 22. The seasonal distribution of nitrate in the natural marsh. All values are monthly averages (h.s.w. - high slack water, l.s.w. - low slack water).

Nitrite concentrations in both areas (Figs.17, 20, 23) were mainly in the range 0-2 ug-at/l, with a few higher values observed in the Murderkill area. Nitrite appeared to show a short period of maximum concentrations in the fall, with minimum concentrations occurring during the summer.

At no time were the marshes found to make a significant contribution of nitrate or nitrite to Delaware Bay. It is hypothesized that organic material containing nitrogen is flushed out of the marsh before sufficient time has elapsed for its oxidation to nitrite or nitrate.

Production and Release of Nutrients from the Sediments of the Tidal Marshes of Delaware

Emmy Lou Gooch

Enumeration of the microbial population

Three different types of salt marsh are represented in this study. Two of these, the natural marsh and the low level impoundment marsh are located on the Murderkill River; and the third, the ditched marsh is located on the Canary Creek at Lewes, Delaware.

Two stations, numbered 2 and 3, were selected in the natural marsh of the Murderkill River. Station 2 represented an area of low, constantly wetted black sediments. Station 3 represented an area of high, drier sediments. Two stations, numbered 5 and 6, were selected in the low level impoundment marsh of the Murderkill River. Station 5 represented an area of low, constantly wetted black sediments; and Station 6 represented an area of high drier sediments. Three stations, numbered 7, 8, and 9 were selected in the ditched marsh of the Canary Creek. Station 7 represented high, dry sediments; Station 8 represented sediments which are occasionally wetted by inundating tidal waters; and Station 9 represented the low, constantly wetted black sediments.

Climax communities are in dynamic equilibrium, with their environment, with a steady-state balance among the constituent species. The composition of the community is rather stable unless external disturbances such as salinity, temperature and pH which are regulated to a large extent by the magnitude of the tides, or exogenous nutrients such as inorganic nitrogen compounds which are carried to the marshes by flooding tidal waters, disturb the equilibrium.

The results of these experiments indicate that the climax type of microbial community occurs within these tidal marsh sediments. Both autotrophic and heterotrophic microorganisms were enumerated. However, heterotrophs of the type which utilize organic carbon in the form of simple sugars such as glucose and lactose, and those of the type which utilize organic nitrogen in the form of simple amino acids predominate.

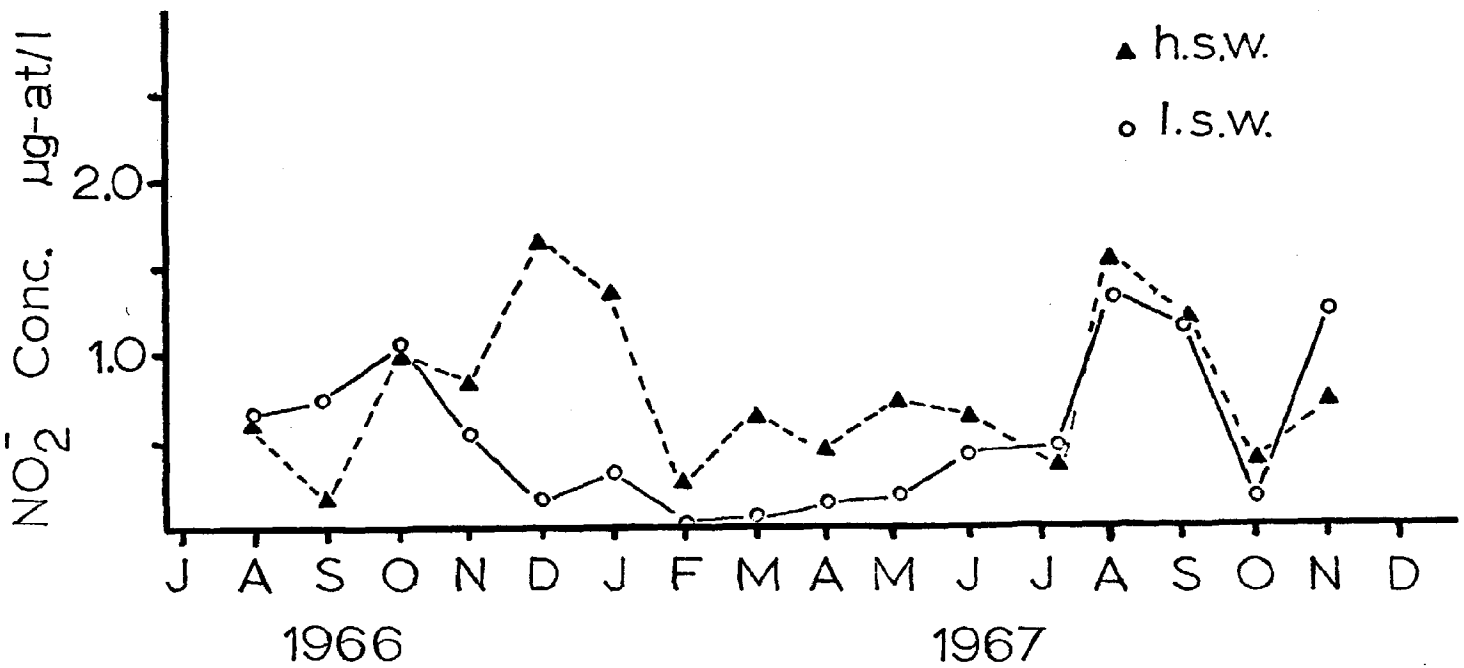

Fig. 23. The seasonal variation in nitrite in the natural marsh. All values are monthly averages (h.s.w. - high slack water, l.s.w. - low slack water).

It appears that the microbial populations of salt marsh sediments vary according to the type of sediment rather than the type of marsh. In all three of the marshes studied the sediments were composed of over 60% water; however, there were visible differences among the surface sediments of all of them. Each of these marshes contains areas of low, black, constantly wetted sediments; and high drier, more sandy sediments. With regard to the physical properties of the sediments of the various stations selected, it can be seen that the salinity of both the sediments and interstitial water is higher in the low, wet areas of these marshes than in the drier areas. Also, the salinity of the sediments of the Murderkill River marshes seems to be constantly lower than that of the sediments of the Canary Creek marsh.

With regard to the total population of microorganisms enumerated from these marshes, the high sediments generally seem to contain more microbes per gram of wet sediment than do the lower sediments. However, this may be an anomaly due to the higher percentage of water in the lower sediments. If this is the case, it may be that at least a majority of the microbial population is bound to the sediment particles and does not live in the interstitial spaces which are filled with water. The exception to this is Station 7 in the Canary Creek marsh which had the drier, sandy sediments but which never had a very numerous total population. In the Murderkill River marshes the total population increased from August to November, 1967. The reason for this appears to be due to an increase in the percentage of the population represented by the coliforms, as well as a slight increase in that percentage represented by the autotrophic nitrifyers. In the Canary Creek marsh the maximal populations were enumerated in the late autumn of 1967 and the early spring months of 1968. Here again the reason for this appears to be due to an increase in the percentage of the population represented by the coliforms and the autotrophic nitrifyers.

The heat resistant (spore forming) microorganisms of the Murderkill River marshes represented about 50% of the population of the low sediments and about 60% of the population of the higher sediments. The same held true for the sediments of the Canary Creek marsh; however, in all cases there were monthly fluctuations. With regard to the aerobic, heterotrophic Bacilli, the sediments of the low stations contained approximately 50%; whereas, those of the higher stations contained approximately 65% of the total population in all the marshes studied.

As was expected, the population of aerobes which included all of the strict autotrophs enumerated in this study combined with that of the facultative anaerobes was in all cases greater than the population of strict anaerobes This latter population included members of the genus Clostridium and Desulfovibrio, both of which have been implicated in the release of inoganic phosphates from the sediments due to their ability to produce hydrogen sulfide (Gooch, 1968 a,b).

It is concluded from the results that throughout the period of this study the microbial communities of the tidal marsh sediments were climax communities. The heterotrophic population of these communities was at all

times greater than that of the autotrophs. The total microbial population of all the sediment types studied maintained itself at a level between one and 33 million organisms per gram of wet sediment. There appears to be no real correlation with either temperature, salinity or pH of the sediments with regard to size or composition of the microbial population indicating an ability to maintain a steady state balance among the constituent species without regard to external disturbances.

However, there was an apparent increase in the percentage of the population composed of the coliforms with increasingly colder sediment temperatures. Also, a higher percentage of the population was represented by the autotrophic nitrifyers during the late winter and early spring months. This may be at least part of the cause of the high winter nitrate levels found by Aurand, 1968 in the tidal waters which inundate these sediments.

With regard to those phosphates released in a soluble form due to the action of acidic by-products of microbial metabolism, it appears that there is a substantial population of these organisms in the sediments. The higher sediments contained a stable population of these organisms which represented about 60% of the total; whereas, in the lower sediments the percentage of the total population represented by these organisms fluctuated from month to month. However, in accordance with previous findings (Reimold, 1965) that soluble inorganic phosphates occurred in the tidal waters in abundance in the winter months, the highest percentage of the total population of these organisms occurred in the late autumn and early winter.

Nitrification

The results of these experiments show that there is net nitrification within these tidal marsh sediments. However, the rate of production varies with sediments collected at different times of the year, with different types of sediments, and with different initial substrates.

The sediments from Station 7 showed good production in the early autumn and early spring using molecular nitrogen and 0.5M NH_4Cl as substrates. However, when 0.5M $NaNO_2$ was the substrate the best production was found with the early spring sediments. The sediments from Station 8 showed maximal production in November and in the early spring using molecular nitrogen and 0.5M NH_4Cl as substrates. When 0.5M $NaNO_2$ was the substrate, maximal production occurred in the late winter and early spring. The low wet sediments from Station 9 showed good production both in the early autumn and early spring with additional good production in the late spring sediments using molecular nitrogen and 0.5M NH_4Cl. Production was maximal in the early spring sediments when 0.5M $NaNO_2$ was the substrate. All three types of sediments showed inhibition of nitrification with increasing concentration of NH_4 substrate. While the initial population of autotrophic nitrifying microorganisms varied with season and sediment type, the generation time of these microorganisms is shown to be faster in all the sediments in the early autumn and spring, correlating with increased rate of nitrification.

Table 6. The maximum and minimum average nitrate concentrations (ug-at/l) and the month of their occurrence over the entire period of this study, high slack water collections. All values are ± 95% confidence interval.

AREA	MAXIMUM CONCENTRATION		MINIMUM CONCENTRATION	
	MONTH	VALUE	MONTH	VALUE
Canary Creek	Feb.	29.14 ± 2.17	July	0.34 ± 0.56
Ditched marsh	Feb.	28.85 ± 1.45	July	0.78 ± 0.49
Murderkill River	Feb.	84.28 ± 27.78	June	1.23 ± 15.81
High level impoundment	Oct.	46.69 ± 16.35	Sept.	3.50 ± 0.43
Low level impoundment	Jan.	69.13 ± 55.36	Sept.	4.12 ± *
Champagne pools	Mar.	36.38 ± 50.21	June	2.93 ± 5.87
Natural marsh	Nov.	100.41 ± 11.91	Aug.	4.21 ± *

* based on only two samples

Table 7. The maximum and minimum average nitrate concentrations (ug-at/l) and the month of their occurrence over the entire period of this study, low slack water collections. All values are ± 95% confidence interval.

AREA	MAXIMUM CONCENTRATION		MINIMUM CONCENTRATION	
	MONTH	VALUE	MONTH	VALUE
Canary Creek	Feb.	32.43 ± 9.67	July	1.08 ± 1.28
Ditched marsh	Mar.	10.35 ± 6.17	July	3.58 ± 2.52
Murderkill River	Nov.	97.20 ± 69.12	Sept.	6.07 ± 11.65
High level impoundment	Oct.	42.31 ± 16.95	Aug.	4.76 ± 0.41
Low level impoundment	Jan.	67.39 ± 22.14	May	5.59 ± 5.50
Champagne pools	Feb.	32.69 ± 24.13	Nov.	3.51 ± 2.70
Natural marsh	Mar.	26.73 ± 34.73	Oct.	4.99 ± 4.72

The pattern of nitrification demonstrated by the closed system method of these experiments was the same for all collections of each sediment type (Fig. 24). Station 7 sediments showed a rapid initial increase of nitrite and nitrate within the first 2-4 days, a short period of denitrification, and then a gradual increase until a peak was reached after 8-10 days. Station 8 sediments showed the same type of initial rapid increase but no real denitrification occurred after this. Instead there was a more gradual increase untill the peak was reached after 6-10 days. Station 9 sediments showed patterns differing with substrate. All substrates produced the initial rapid nitrification, however only the 0.5M NH_4Cl substrate showed gradually increased production without any denitrification for the first five days. After 6-7 days peak values were reached with the molecular nitrogen and NH_4Cl substrates; however a peak was not reached until 11-12 days with the $NaNO_2$ substrate. This latter substrate also showed a period of denitrification after 6-7 days.

Although nitrite and nitrate were produced in these experiments at the same unit concentration as that found by Aurand (1968), these results seem to contradict his findings in that he found maximal nitrate concentrations during the winter months; whereas, these experiments show maximal production in the autumn and spring months. However, since there is no appreciable growth of nitrate utilizers in the winter months, the autumn production is probably not used and accumulates through the winter. The spring nitrate production, while initially large as compared to that of the winter, is probably used by growing plants allowing little to accumulate during the spring and summer months.

It has been shown that nitrite accumulates only when some ammonia remains and this accumulation is favored by alkaline conditions. This probably results from inhibition of nitrite oxidizing microorganisms such as Nitrobacter which are sensitive to ammonia under alkaline conditions. These experiments show that at all stations the early autumn sediments had an initial accumulation of nitrite which was overcome after 4 days by the production of nitrate when 0.5M NH_4Cl was the substrate. The spring sediments did not show this with the single exception of the sediments collected in May from Station 7.

Work has demonstrated that within the sediments ammonia is bound to the particles and it is here that nitrification occurs. It has also been shown that organic nitrogen compounds were first attacked by organisms which acted to cause the release of ammonia. This ammonia was then converted to nitrite and nitrate by the nitrifying autotrophs. If the release of nitrogen from the tidal marshes is from organic nitrogen as postulated by Aurand (1968), then conversion to ammonia and thence to nitrate must take place on the detrital particles in the water. When nitrate was formed it would then be utilized by the water flora and any excess would return to the marsh with the flooding tide. Thus, the marsh would receive from, as well as contribute to, the nitrogen budget of the estuary.

It is concluded from the results of these experiments that nitrification takes place in the sediments of the Canary Creek marsh at rates differing with sediment type and initial substrate, but at a magnitude

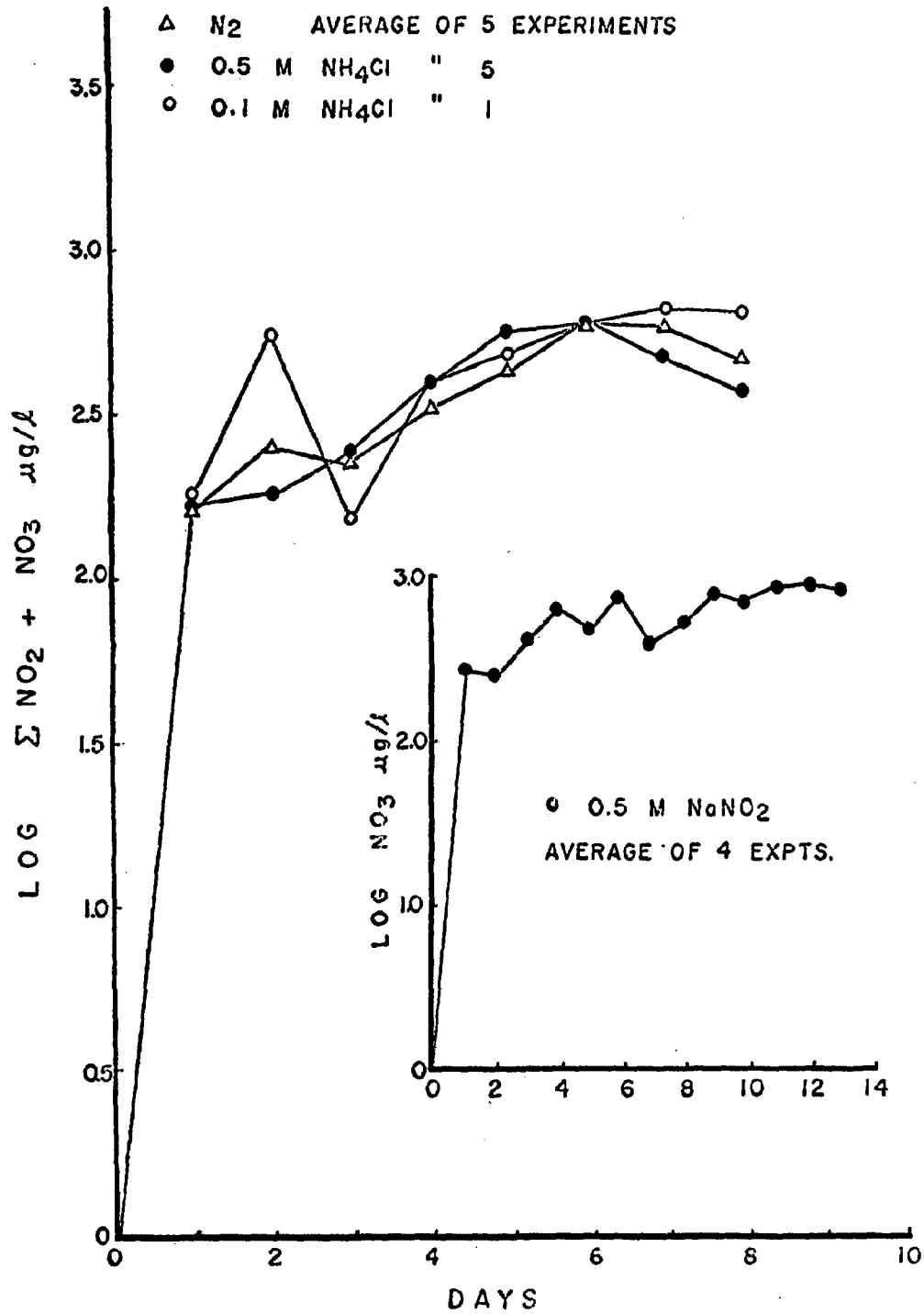

Fig. 24. Nitrification in the sediments at Station 9.

sufficient to supply the needs of nitrate requiring flora. The most rapid nitrification occurs in the autumn and spring months, and accumulation of nitrate occurs during the winter months because that produced is not used; whereas, there is little accumulation in the warmer months due to utilization by the marsh flora. It is possible that the inorganic nitrate produced within the marsh sediments is used exclusively by the marsh flora and very little is available for release to the Delaware Bay. Since flooding tidal waters contain as much or more inorganic nitrate than do ebbing tidal waters, it is possible that it is produced from organic nitrogen exported as detritus from the marsh and that nitrate not used by the estuarine flora is brought back to the marsh where it supplements the marsh production and is used by the marsh flora.

PRODUCTION AND UTILIZATION

Annual Angiosperm Production

Marcia H. Morgan

Quantitative measurements were made in selected areas on the Canary Creek salt marsh to determine the quantity of angiosperm plant material produced during the 1960 growing season. Production was measured by the clip quadrat method. Preliminary analysis demonstrated that 24 half square meter samples were adequate for each sampling date.

The production as determined by this treatment of the data is an estimate of the net production of the angiosperms. It does not include the amount of meterial used in maintenance and building new roots, lost through respiration, eaten by herbivores such as Sesarma reticulatum, the marsh crab, or carried away by the tides during the summer months. Net production is represented as the sum of the amount of living material present at the end of the growing season and the increase in dead material during the growing season (Table 8, Fig. 25).

The marsh was found to produce 445 grams at a rate of 5.32 grams per day of dry weight per square meter. Production was found to vary over the surface of the marsh and was associated with drainage conditions.

According to the computed growth curve (Fig. 25), the growing season started in mid-May, but from observation it is more likely that it started in April. The end of the growing season is marked by a decrease in the quantity of living material. By the first week in September, most of the plants started flowering and seed production was completed by the beginning of October. Undoubtedly photosynthesis continued during the fall months, but the rate of catabolic activity exceeded the rate of anabolic activity so there was a net decrease in dry weight.

The roots of the monocotyledons (Spartina and Distichilis) survive the winter months in this climate, and much of the current crop grows from the root systems of previous years. The weight of the roots was not included although this introduced an error into the data. It would have been difficult

Table 8. The average dry weights with standard errors of 24 samples for each collection date.

Date of Collection	Average dry wt. in grams of ½ sq. meter Living	Dead	Total
June 20	90.2±10.0		
July 6	141.7± 9.6	78.3± 9.0	220.0±17.0
July 15	127.6±10.6	117.5±13.0	245.1±17.8
July 20	165.2±12.1	103.8±11.3	269.0±19.7
August 4	173.4±13.4	71.4± 9.7	244.8±20.2
August 20	185.6±17.1	76.7±12.0	262.3±25.0
September 1	206.9±16.9	93.7± 9.2	300.6±22.5
October 3	176.4±12.8	97.0± 7.7	273.4±16.1

*Represents the sum of the green material and the dead material which apparently was part of the current season's crop.

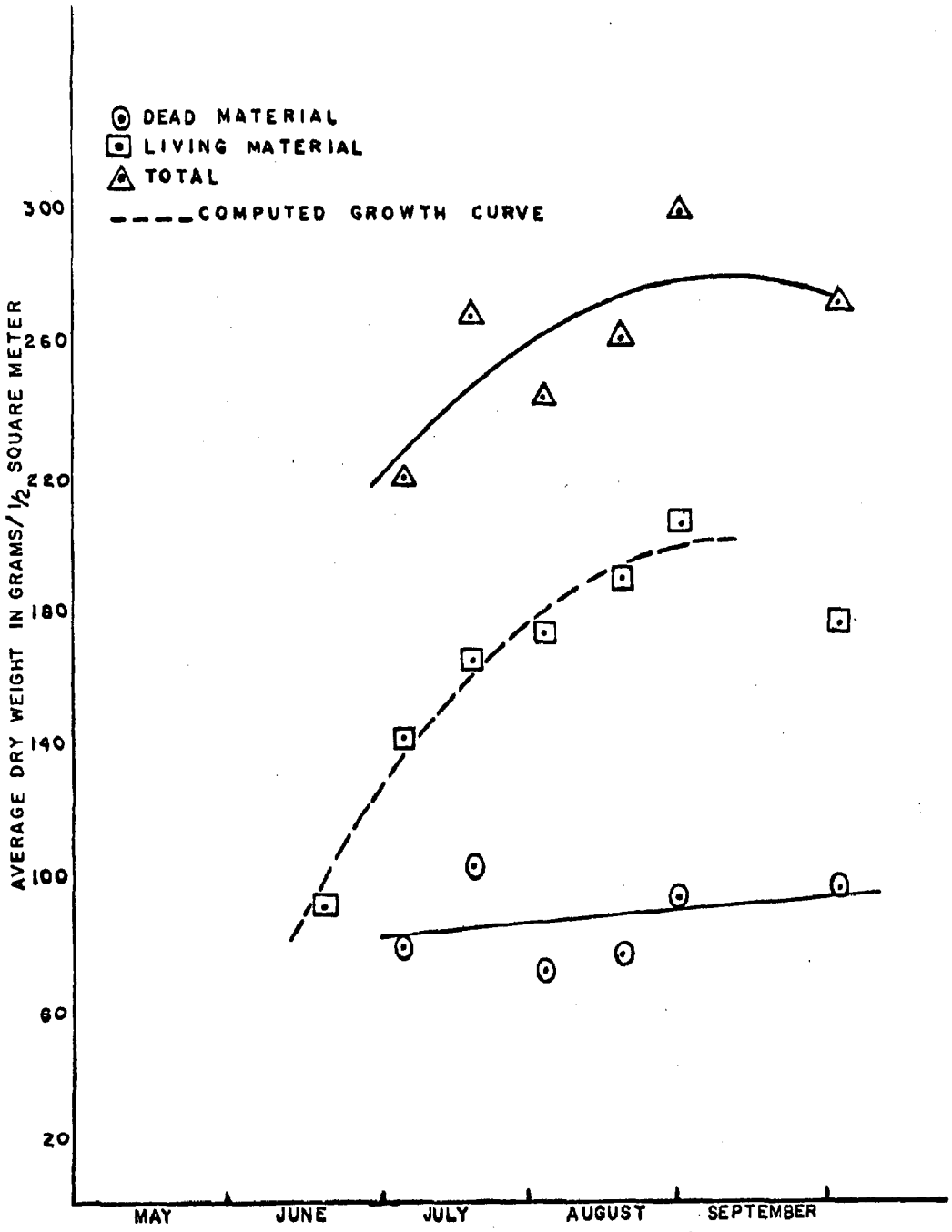

Fig. 25. The average dry weights of material collected and the computed growth curve.

to determine which, if any, of the plants had started this year and which were growing on the roots of other seasons.

Herbaceous plants such as the angiosperms on the Canary Creek marsh usually have a growing season or turn-over rate of one year; one and only one crop which does not carry over through the winter months is produced each year. Determination of the amount of living material however, was complicated by a growth characteristic of these plants. Some, but not all, plants survive the winter in such a way that the inner, growing tissues are green and active the following year. This results in a plant composed of material from at least two growing seasons.

Twice a day the tides rise up on the marsh and then recede carrying away dead or decaying plant material. Rain and wind accentuate the process by bending the plants so that they are more likely to be picked up by the flooding waters. Undoubtedly most of the plant detritus carried out is dead material from earlier seasons. However, as these plants typically grow in such a way that the lower leaves are continually dying, some current production may also be exported.

When the various factors which lead to the loss of production are considered, 445 grams of dry weight per square meter is a low estimate of the amount of new protoplasm which is made available to the herbivores, carnivores, and decomposers of the ecosystem. That which is not used in the marsh itself will be carried out into the bay to feed or provide nutrients for the organisms living there.

Caloric Studies of *Spartina* and the Marsh Crab *Sesarma Reticulatum* (Say)

Oliver Crichton

The caloric studies described have been preceded by four summers (approximately six weeks each) spent in studying the life history of the marsh crab. From these studies it has become apparent that *Sesarma*, as it occurs in the estuarine waters of Delaware Bay, is always found associated with the marsh grass *Spartina alterniflora* and in close association with the fiddler crab *Uca pugnax*. The large burrows of the marsh crab are found within five meters of the tidal water and often are interconnected by the smaller burrows of the fiddler crab. Unlike the marsh crabs' burrows, however, the burrows of the fiddler crab extend much farther back from the open tidal water and occur throughout the *Spartina* community.

During the summer months the marsh crab's primary source of food appears to be the leaves of *Spartina*. Evidence gathered seems to indicate that extensive areas of *Spartina* growth along the mud banks of marsh creeks and drainage ditches are reduced to stubble much like a cut-over field of corn.

From these observations it has seemed reasonable to make some tentative hypotheses in terms of the relationship of the marsh crab to the whole marsh and nearby estuary. For one thing the extensiveness of the burrowing activity

plus the elimination of patches of Spartina must encourage erosion by tides and currents, causing the creek banks to crumble. Secondly, the marsh crab itself, by its constant feeding activity, leaves some pieces of torn and shredded Spartina to be washed away by the tide along with the fecal remains of the Spartina it has ingested, thus directly contributing organic detritus through the action of the tidal currents to the estuary.

It was in connection with the grass actually consumed by Sesarma that the first caloric studies were attempted in the summer of 1965. During this investigation the crabs were brought into the laboratory and kept in containers with a small amount of sea water. Daily they were fed weighed amounts of fresh green Spartina and all unconsumed grass and fecal material were collected and dried. Energy determinations of the dry Spartina were carried out with no difficulty, but due to the presence of the sea water all fecal material after drying contained too much salt to ignite. Similarly attempts to ignite the dried crabs themselves proved unsatisfactory, probably due to both the presence of salt and the calcareous exoskeleton. Caloric determinations made on fecal material at this time were carried out only after the salt had been dissolved in water and removed by filtering, and since other materials were lost at the same time, these results were not considered valid.

In a second attempt to gather some meaningful data on the energy flow from the Spartina through the marsh crab the following procedure was undertaken. Thirty-five adult male crabs, ranging in carapace width from 22-32 mm., were collected in Canary Creek marsh and transported to the laboratory in an insulated carrier kept cool with a small amount of ice. Each crab was placed in an individual covered plastic container measuring approximately 15 cm. in diameter and 15 cm. high. In addition 15 gallons of sea water and several plastic pails of whole Spartina plants, including roots, were brought back to the laboratory and kept in a basement room where the temperature remained between 25° and 30°C.

Each crab was washed in clear sea water to free the body of mud and then returned to its plastic container. A weighed quantity of fresh Spartina cut in 6 cm. lengths was placed in the container with the crab, and the cover fitted tightly to prevent loss of water by evaporation. By this means it was found possible to keep the animals alive and feeding without adding any sea water which had previously been considered necessary, and thus obtain feces containing a minimum of salt.

The crabs were removed daily from their containers one by one and placed in fresh sea water so that they had a chance to re-fill their gill chambers. All feces were removed with a rubber policeman, consolidated in an evaporating dish and placed in an oven (100°C.) to dry. The unconsumed Spartina was collected, consolidated, and placed in the oven. All containers were then rinsed in sea water and each crab returned to its container along with fresh Spartina. In preparing the fresh Spartina each day, three lots, each consisting of approximately 210 six cm. pieces of cut grass blades, were weighed; two of them were placed in the oven and dried for a fresh dry conversion factor determination, and the other was divided among the 35 crabs. This part of the procedure was continued for about fifteen days after the initial collection of grass and crabs.

The samples collected for dry mass determination of fresh Spartina, the Spartina offered but not consumed by the crabs, and the daily fecal collections were weighed. The dry grass samples were then ground in a Wiley mill and all samples placed in tightly covered glass bottles in readiness for calorimetry. All samples were run in duplicate with per cent of error between samples ranging from 0.1 - 4.7% and averaging 1.8%.

Fecal collections from the first few days were the first samples tested, because at this point it was still not known whether or not their salt content was going to be too high for combustion. All went well, however, indicating that the moist container lacking added sea water had been successful. In addition samples collected during the period July 9, 1966 - July 12, 1966 were not used. First, it was felt that for the first two days fecal collections were in all likelihood related in part to food consumed by the crabs in the marsh before they were collected. Secondly, some of the fecal collections were irretrievably lost due to the malfunctioning of the calorimeter.

The utilization efficiency of what was offered the crab was determined by calculating the total energy offered the crabs each day, the total energy unconsumed, and the total energy in the feces based on the total dry weights and calories per gram in each case. Thus it was possible to arrive at the total energy utilized by the crabs by subtracting from the total energy offered the sum of the total energy unconsumed plus the total fecal energy divided by the total energy offered. This has been expressed as a per cent in each case (Table 9 and Fig. 26) with an average of 18 percent.

The utilization efficiency of what the crabs ingested was determined by dividing the total energy assimilated by the total energy ingested (feces plus assimilated). This has been reported in Table 9 and Figure 26 with an average efficiency of 58 percent.

From the nine day period examined it would appear that 42 percent of the energy harvested by Sesarma is passed directly to the marsh surface in fecal deposits. Since the fecal pellets which have been collected in the marsh contain discrete pieces of Spartina it seems reasonable to predict that these grass "cuttings" float to the surface during the periods of tidal flooding and are carried away as the tide recedes.

Another aspect of these experiments is the indication of a possible cyclic nature (Fig. 26) in feeding activity of Sesarma. In spite of the salt problems calculated utilization efficiencies in 1965 show a similar range and cyclic pattern with an overall average of 12 percent as compared to 18 percent for 1966.

DISCUSSION

The hydrography of tidal creeks has a profound influence on the ecology of tidal marshes and the organisms living therein. The smaller streams and guts are essentially drained on each ebbing tide and refilled on the next flood. In the larger tidal streams the flooding tide acts as a ram filling the lower reaches of the stream and holding the fresher water in the upper

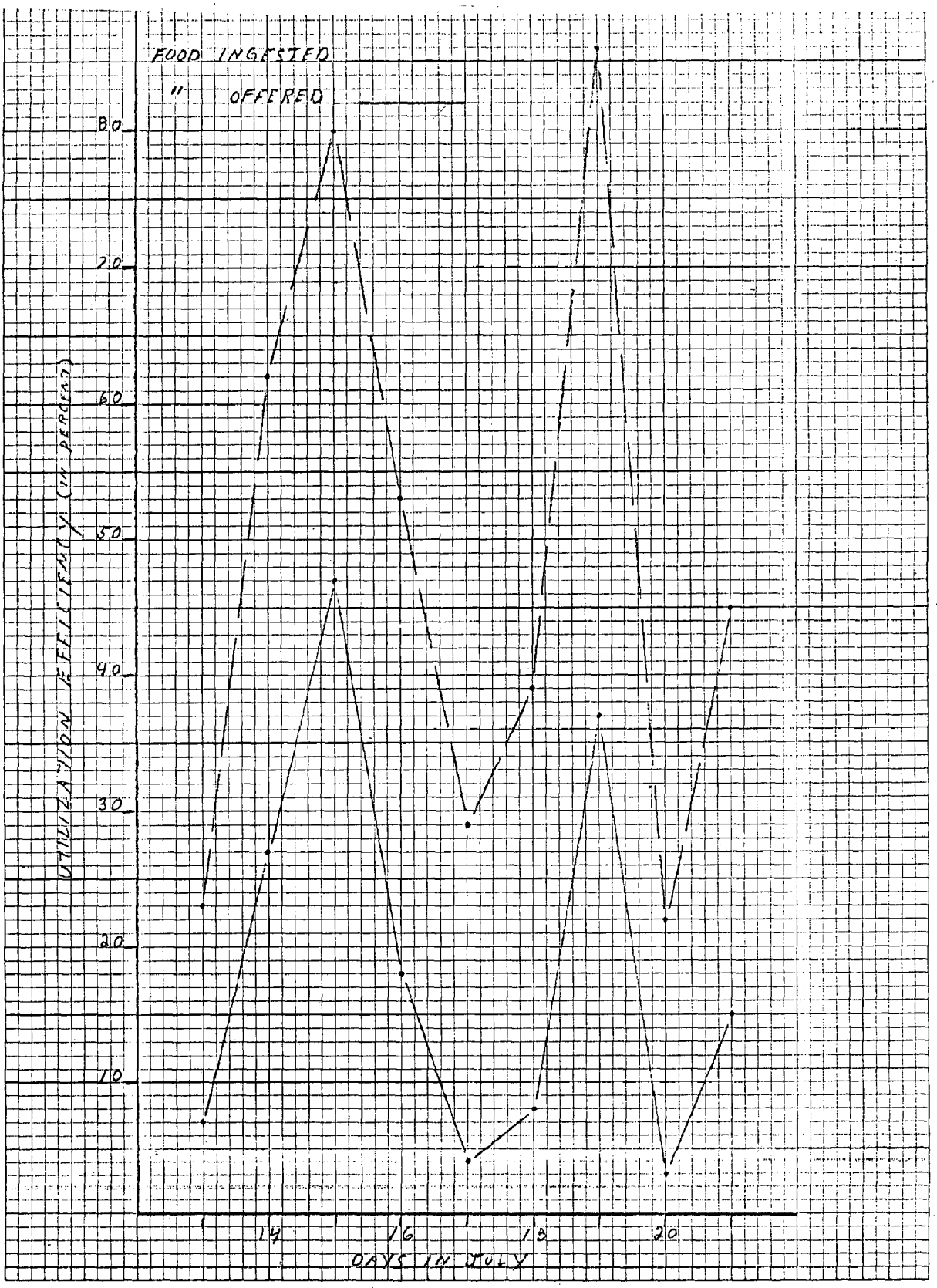

Fig. 26. Energy uptake by 35 adult male Sesarma reticulatum consuming Spartina alterniflora during July 13-21, 1966.

Table 9. Energy uptake by 35 adult male *Sesarma reticulatum* consuming *Spartina alterniflora* during July 13-21, 1966.

Date	Dry wt. (gms) consumed		Total Energy in Calories				Utilization Efficiency (in percent)	
	Total Day	Day Crab	Offered	Unconsumed	In Feces	Assimilated	Offered	Ingested
13 July	0.70	0.020	8380	5771	2020	589	7	23
14 July	0.80	0.023	12600	7011	2140	3449	27	62
15 July	1.37	0.039	10100	4193	1164	4743	47	80
16 July	0.89	0.025	12500	8267	2000	2233	18	53
17 July	0.07	0.002	14900	12730	1530	640	4	29
18 July	0.47	0.013	12500	9988	1530	982	8	39
19 July	0.55	0.016	14800	8522	877	5401	37	86
20 July	0.32	0.009	14600	12900	1320	380	3	22
21 July	0.92	0.026	12300	8000	2360	1940	15	45
Average	0.68	0.019	12520	8598	1660	2262	18	58

reaches of the stream. Although the net flow is downstream there are distinct regions with decreasing current velocities upstream. This will have a marked influence on the rates of downstream transport of nutrients, organisms, fresh water or pollutants.

The waters of a tidal marsh carry greater nutrient loads than other environments reported so far. Such levels may be brought about by an accumulating and holding action natural to such marshes or resulting from various forms of man-induced eutrophication of the marshes, adjoining uplands and the streams themselves.

The accumulating and subsequent releasing action appears to result from a very complex interaction of numberous factors. The microbial populations appear to be a very important component. The delicate balance set up by their interactions with the mineral content of the soils in conjunction with changes in acidity-alkaline levels under aerobic-anaerobic conditions will determine the release or binding of important nutrients such as phosphorus. Although there is a net downstream discharge of phosphorus at a high level, there is a continuous accumulation of this element in the marsh soils.

The seasonality of nutrient levels also poses interesting problems. The high levels of phosphorus in the marsh waters during the warm months suggests the release of greater quantities of this nutrient in spite of the greater metabolic levels brought about by higher temperatures. All of this is in contrast to the reduced levels of nitrogen found during the warm months and high levels during the winter. This is in spite of the same high metabolic demands for nitrogen brought on by the same temperature levels effecting phosphorus uptake.

While there is a net downstream flow of phosphorus there is essentially a zero net movement of nitrogen. This, in conjunction with the reversed seasonal phasing of these two cycles and the recorded levels of both nutrients, would suggest that nitrogen could possibly be a limiting factor rather than phosphorus, especially during the summer. This is particularly interesting in light of the known eutrophication that occurs in some tidal streams with greatly reduced oxygen levels.

Man's manipulation of tidal marshes can have an explicit effect through ditching or impoundments by tending to reduce the release of nutrients by altering the tidal exchange as compared to a natural marsh. On the other hand, the creation of anaerobic conditions through organic eutrophication could tip the delicate balance toward the enhanced release of critical elements such as phosphorus.

The nutrient loads in tide marsh waters point to high productivity. This is substantiated by the quantities of rooted vegetation that can be harvested from the surface. The value of this vegetation is greatest after it dies and is degraded to detritus. This degradation process is enhanced by the feeding habits of organisms such as marsh crabs where nearly half the energy ingested is lost in the form of feces which contribute to the detritus load transported into the adjoining estuarine and coastal waters.

The tidal marsh is an ecological ecotone between the uplands and the estuarine and coastal waters wherein exists a very delicate and complex balance of accumulation and release. This balance can all too easily be upset by environmental changes, natural or man-induced.

Utilization by Man

Salt marshes give rise to mosquitoes and biting flies that make life miserable; they are filled with a sticky, odorous mud that clings to boots and clothing. Most people stay away from coastal marshlands, yet hunters and trappers know well that these regions can provide sport, food, or a considerable financial yield. Fishermen find they can catch snapping turtles, diamond back turtles, blue crabs, oysters, white perch, and other fishes in the tidal streams that wander through marshland. Furthermore, biologists are becoming aware of the important role salt marshes play in the biotic economy of coastal waters.

Tidal marshes may be used in different ways. They can be receptacles for the discards of man's activities - tin cans, old cars, refrigerators and other rubbish that blight the landscape. This refuse, levelled off and packed down becomes an industrial plant site or perhaps a new housing development.

Filled-in and polluted marshes cannot perform their natural role. Our expanding population with all of its associated needs for more land and new sources of food has created an interest in tidal marshes. The need for man-made changes in coastal lands is obvious, but what of the natural role of marshes? Here is a matter of conflicting interests.

Ever since man has been a hunter he has known that ducks and other animals can be taken from tidal marshes for food; now hunting and fishing for recreation replace the need for food. Conservation departments must maintain maximum levels of wildlife resources in ever diminishing marshland for increasing numbers of sportsmen.

More people, with more money and time available, are looking to the seashore as a place to spend their vacations. Naturally they are annoyed by anything that will cause undue discomfort during this time: their ire increases in direct proportion to the number of mosquito bites they receive. The proprietors of seashore vacation industries are disconsolate when visitors leave ahead of schedule. State and federal agencies have tried to do something about mosquitoes and biting flies. Ditches are dug to drain the marshes to reduce the mosquito breeding sites; potent insecticides are sprayed over wetlands and adjoining areas to knock out mosquitoes that survive the results of ditching. A newer attack, impoundment of water over swampland areas, is now being tested as a means to control the salt marsh mosquito, *Aedes sollicitans*, and also to enhance these areas for water fowl and other wildlife.

There are now fewer acres of tidal marsh than in former years, yet there are more people who want to get something from these acres - more ducks, muskrats, raccoons, turtles, fish, crabs, and oysters. Since most

of these animals are also taken in bays and estuarine areas adjoining wetlands, it is natural to wonder what and how much the marshes contribute to the biological economy of regions like Cape Cod, Gardners Bay on Long Island, Delaware Bay and the coastal areas of the Carolinas, Georgia and the Gulf States. In recent years investigators have been seeking answers in the marshes of New England, Long Island and Georgia, to name only a few places.

Acknowledgment

The work described here was begun as an ecology class project in the spring of 1959 and aided by the Fish Ecology course, and by research assistants: Lee Miller, Kent Price, and Paul Wolf in the ichthyoplankton; Wallace de Witt (Master's thesis), study of the hydrography of the Broadkill and Murderkill Rivers; Robert Reimold (Ph.D. dissertation), phosphorus cycles in tidal marshes; Maureen Gorman (senior special problem), inorganic phosphorus concentrations in marsh soils; Emmy Lou Gooch (Master's thesis), hydrogen sulfide and inorganic phosphate release in marsh sediments; Don Aurand (Master's thesis), nitrate and nitrite cycles in marsh waters; Emmy Lou Gooch, microbial populations and nitrification in marsh soils; Marcia Morgan (Master's thesis), angiosperm production in tidal marshes; Oliver Crichton, caloric studies of *Spartina* and the marsh crab *Sesarma*.

Financial aid was received from the Delaware Game and Fish Commission, University of Delaware Water Resources Council, and the University of Delaware Research Foundation.

Chapter C-4C

IRREGULARLY FLOODED MARSH

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INTRODUCTION

In the southeastern states of the United States in broad expanses is a special type of salt marsh that is only irregularly flooded with salt water and is composed mainly of a tall dark rush, Juncus roemerianus. This ecosystem type is much involved in controversy because of salt water mosquitoes which develop in its temporary brackish pools. Various management efforts such as ditching, spraying and impounding are being tried by state agencies in an effort to control the mosquitoes.

Tidal inundation is a major factor influencing the distribution of marsh species. Marshes that are normally flooded at every high tide are termed regularly-flooded. Marshes that are flooded as a result of spring, wind or storm tides are termed irregularly-flooded.

In recent years considerable research has been done on the regularly-flooded salt marshes in the United States (Odum, 1961; Teal, 1962; others), but very little on the irregularly-flooded salt marshes. Significantly lacking are studies on the nutrient and energy exchanges between irregularly flooded salt marshes and the nearby estuaries.

Along the South Atlantic and Gulf coasts irregularly-flooded salt marshes are usually dominated by Juncus roemerianus at lower elevations and by Spartina patens and Distichlis spicata at higher elevations. These marshes are usually best developed in areas behind barrier islands and away from inlets, along the fringes of large brackish embayments and alongside the lower reaches of creeks and rivers. Good examples of this type of marsh are seen in the Pamlico Sound area of North Carolina, from Cedar Keys to Apalachee Bay in Florida, and near the mouth of the Mississippi River.

The irregularly-flooded salt marshes cover vast areas. For example, in North Carolina these marshes cover 205,750 acres, while regularly-flooded marshes cover only 58,400 acres (Wilson, 1962).

EXAMPLES

Studied examples are introduced next from each of three areas: North Carolina, Florida, and New England.

* On Leave from N.C. Dept. of Conservation and Development

Bodie Island, North Carolina

Waits (1967) surveyed the irregularly-flooded salt marshes of Bodie Island, and defined six major vegetation types for those marshes. Table 1 includes data on the species composition and percentage of cover for each vegetation type. Figure 1 shows their horizontal relationships. The Juncus roemerianus is mainly concentrated along the tidal creeks, but small clumps occur away from the creeks.

Beaufort, North Carolina

During a recent preliminary survey of the marshes along the upper reaches of the North River near Beaufort, North Carolina (Fig. 2) I found Juncus to be the dominant marsh plant. A cross-section through a typical Juncus marsh was examined along a freshly-dug mosquito-control ditch. Near the river there was a slight natural levee approximately 15 cm. above the level of the Juncus marsh and about 15 m. wide. The Juncus marsh then extended 700 m. to a 15 m. wide fringing marsh of Distichlis spicata and Spartina patens. At the time of observation the tide was high and the water level was below the level of the marsh, thus affording a good opportunity to judge elevation differences. There was no observable difference in the elevation along the 700 m. width of the Juncus marsh, the water level being approximately 5 cm below marsh level at all points.

The material in the spoil piles along the length of the ditch gave evidence of the underlying substrate. There was a layer of fibrous peat under the marsh and this became progressively thinner near the woods and underlain by sand. Also, there was an occasional stump showing along the edges of the ditch. I interpreted the presence of the sand-marsh facies and the stumps to mean that the marsh was invading the woods. Kurz and Wagner (1957) found a number of similar facies in their studies of marshes in Northwest Florida (Fig. 3).

Live Oak Point, Florida

Figure 4 (Kurz and Wagner, 1957) shows the horizontal distribution of regularly and irregularly-flooded salt marsh plants at Live Oak Point, Florida. The authors suggested that the small differences in elevation were responsible for most of the vegetation patterns. They reported that the sea level was rising faster than aggradation and marsh vegetation was undergoing considerable succession.

Table 1. Vegetation types of the Bodie Island marsh showing major species and percentage of cover of each type. After A. W. Cooper (Waits, 1969).

Vegetation type	Major species	Percentage of cover
Type 1	Spartina patens, Distichlis spicata, Scirpus robustus	32
Type 2	Same as Type 1	26
Type 3	Juncus roemerianus	9
Type 4	Eleocharis flavescens, Spartina alterniflora, Salicornia spp.	9
Type 5	Spartina patens, Distichlis spicata, Scirpus robustus with Eleocharis tuberculosa, Kosteletzkya virginica, Lythrum lineare, Scirpus americanus, Typha spp.	23
Type 6.	Cyperus odoratus, Cyperus filicinus, Echinochloa walteri, Eleocharis albida, Spartina patens	11

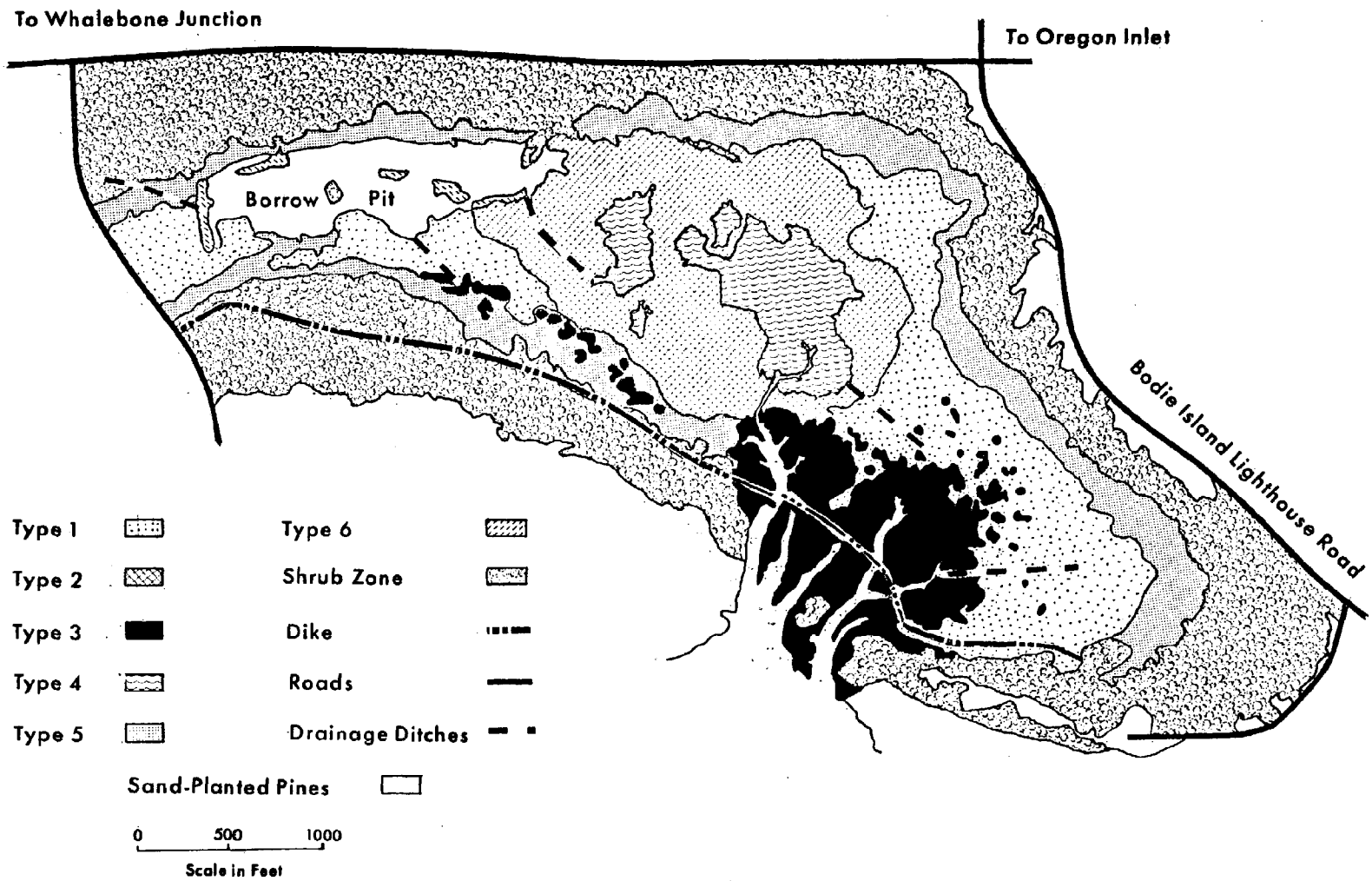

Fig. 1. Six vegetation types in the Bodie Island marsh: Type 1 - Spartina patens Type; Type 2 - Mixed Type; Type 3 - Juncus roemerianus Type; Type 4 - Open Water Type; Type 5 - Marginal Type; Type 6 - Bare Sand Type. (Waits, 1967).

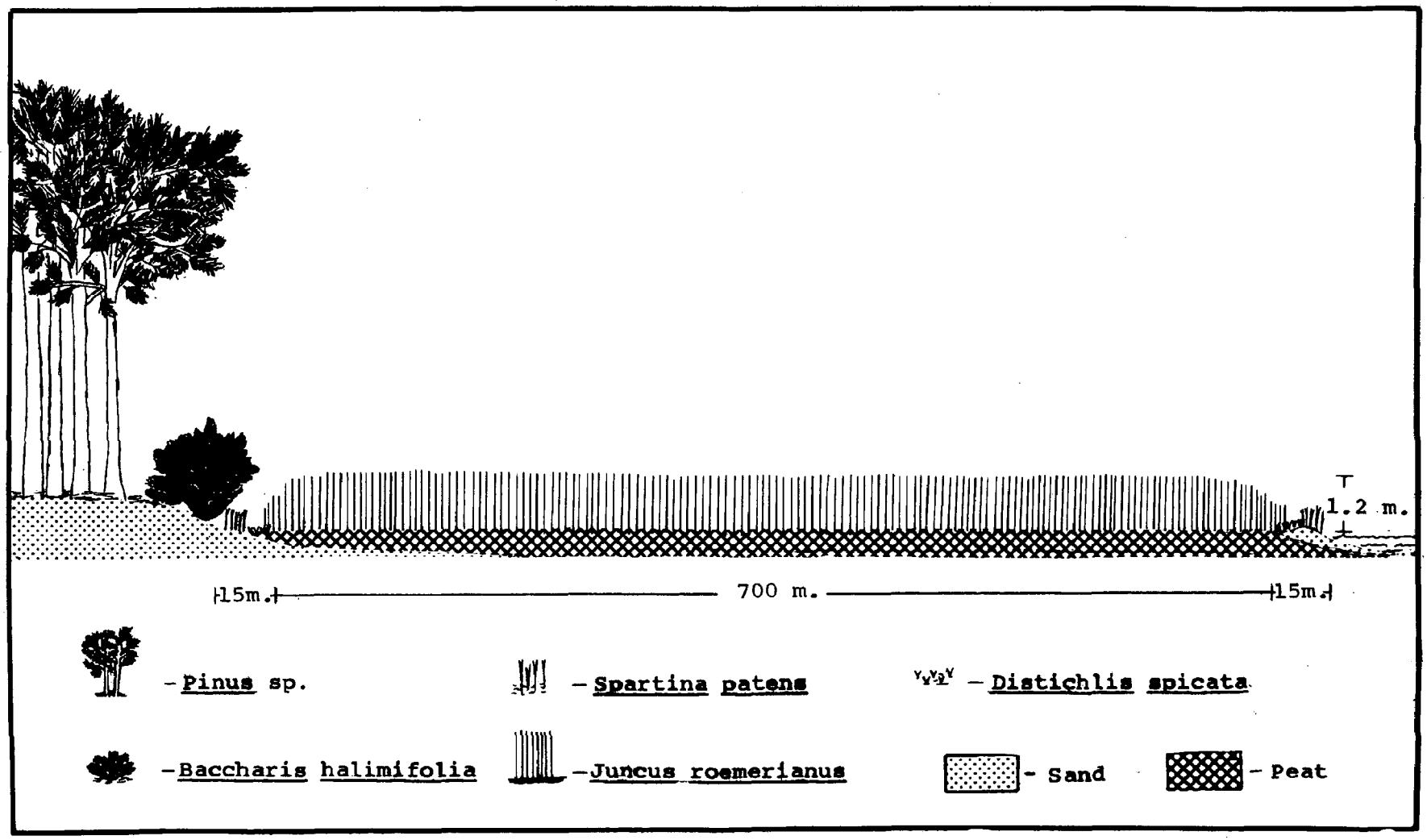

Fig. 2. Diagrammatic cross-section through a Juncus roemerianus marsh on North River, near Beaufort, North Carolina. Vertical scale exaggerated.

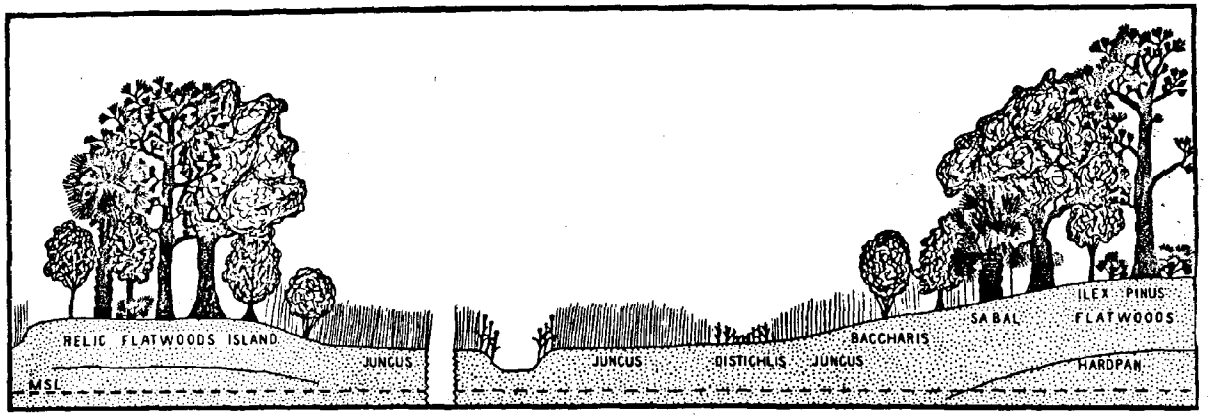

Fig. 3. Cross-section through a Juncus marsh at Shell Point, Florida, showing pure stands of Juncus at lower elevations and fringing Juncus invading the flatwoods (Kurz and Wagner, 1957).

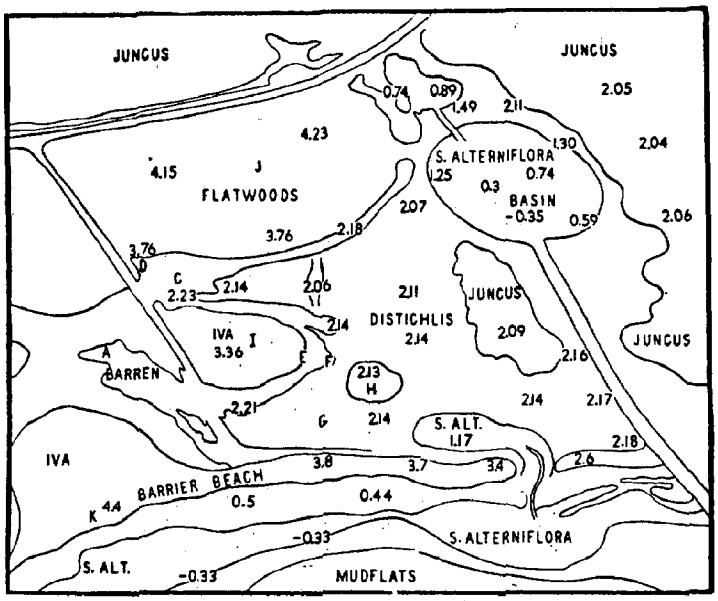

Fig. 4. Horizontal distribution of regularly-flooded and irregularly-flooded salt marsh plants at Live Oak Point, Florida. Figures are elevations (ft.) above mean sea level. (Kurz and Wagner, 1957).

New England

The irregularly-flooded salt marshes of New England are dominated by Spartina patens at lower elevations and by Juncus gerardi at higher elevations. Cooper, in Chapter C-4A of this publication, presents excellent diagrams (Figs. 13 and 14) showing the vertical distribution of New England marsh plants. In Figure 15 Cooper shows the horizontal distribution of New England marsh plants.

DOMINANT SPECIES, JUNCUS ROMERIANUS

Although published ecological literature on irregularly-flooded salt marshes is extremely limited, the role of one species, Juncus roemerianus, has received more attention. The following is a summary of the recent research on this species.

Distribution

Juncus roemerianus occurs in the coastal marshes of the United States from Maryland to Texas (Gleason and Cronquist, 1963). Foster (1968) has suggested that Juncus covers more area in North Carolina than any other marsh species. He found Juncus to be the dominant plant species in the marshes of the upper reaches of the Lockwood Folly River in North Carolina (Figs. 5 and 6). Kurz and Wagner (1957) found it to be the dominant marsh plant in northwest Florida, but of less importance in the Atlantic coast marshes of northern Florida and in the vicinity of Charleston, South Carolina. Davis (1943) found it to be an important species in coastal marshes of southwest Florida, but replaced in most salt marshes in that area by mangroves. Egler (1952) suggested that salt marsh vegetation in southwest Florida is a pioneer post-hurricane growth which is quickly invaded by woody plants. He reported that Juncus was a temporary dominant in some areas where the mangroves had been killed by hurricanes. Penfound and O'Neil (1934) found Juncus to be the dominant species in the marshes around Cat Island, Mississippi.

Habitat Factors

The salinity of the marsh habitat is a function of the salinity of the overlying water, the relative frequency and duration of inundation and the rate of flushing through the soil.

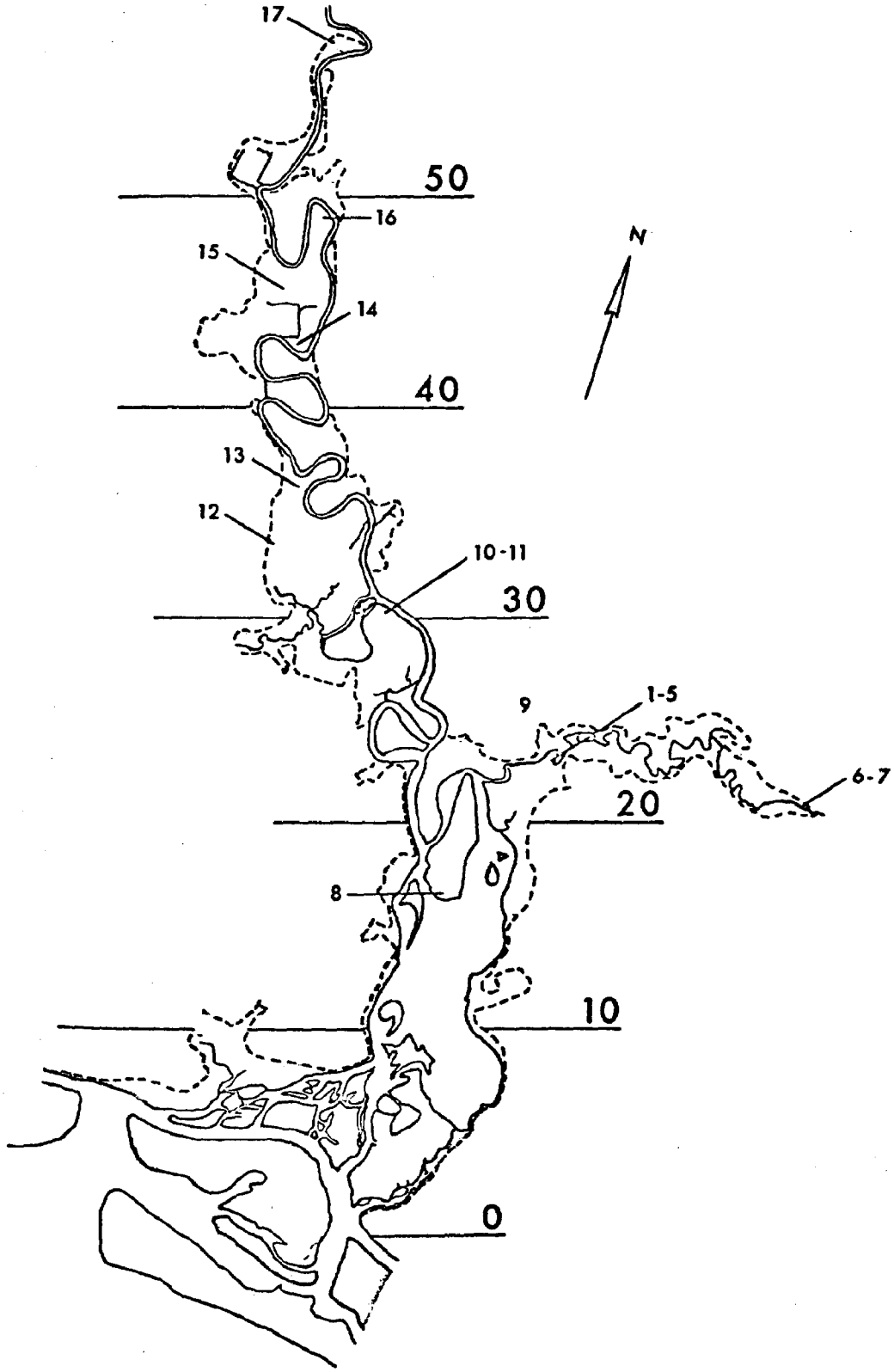

Fig. 5. Map of the Lockwood Folly River showing placement of transects and locations of sample points (Foster, 1968).

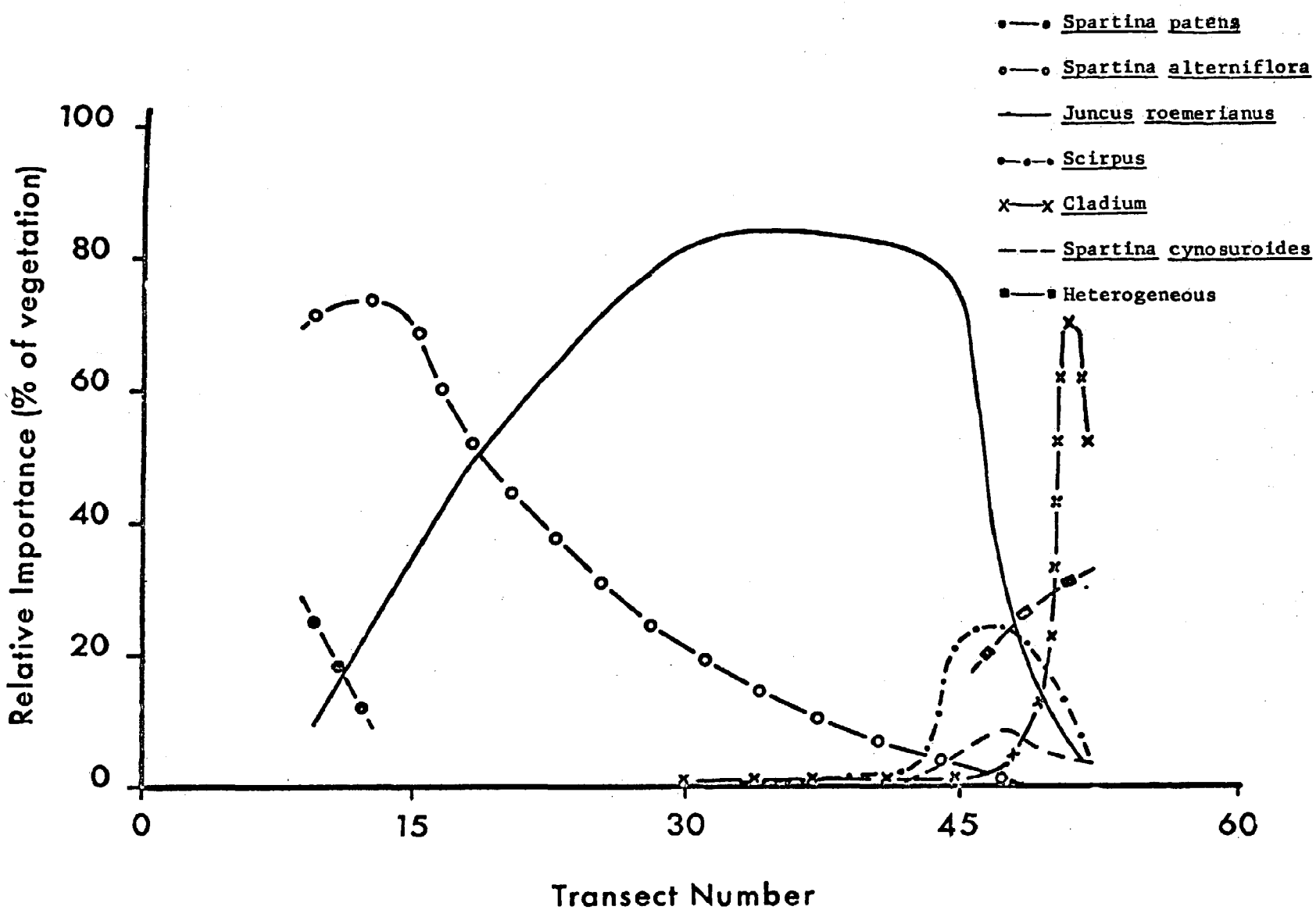

Fig. 6. Distribution and relative importance of the major marsh vegetation types on the Lockwood Folly River (Foster, 1968).

Penfound and Hathaway (1938) reported that although Juncus marshes in Louisiana occurred from 1.2 - 43.3 $^{0}/_{00}$, they were best developed where the salinity of the overlying water in the marsh was 5 - 20 $^{0}/_{00}$. Soil water salinity in a Juncus marsh in South Carolina was reported by Stalter (1968) to range from 1 - 26 $^{0}/_{00}$. Foster (1968) studying the Juncus marsh at Lockwood Folly River, North Carolina, found that the salinity ranged between approximately 5 and 82 % sea strength, and that a decrease in soil salinity upstream was closely correlated with a decrease in the abundance of Juncus (Fig. 7). Juncus was the dominant marsh plant from transect 19 through 46 (Fig. 5). The transects were 500 feet apart; consequently Juncus was the dominant marsh plant for more than 2.5 miles along this river. Davis and Gray (1966) described similar Juncus marshes along tidal rivers in Carteret County, North Carolina.

Seibert (1969) reported that germination of Juncus seeds was delayed by increasing salt concentrations and did not occur in 72 days in sodium chloride concentrations above 1% (Table 2). Germination in sea water and in sodium chloride at the same concentrations was similar at the end of 21 days (Table 3). When the ungerminated seeds from all the sea water dishes were transferred to distilled water, germination levels in all samples exceeded 75% (Table 3).

Vertical Range

Juncus grows at elevations from mean high tide to above the spring tide level. Adams (1963) reported clumps of Juncus in Spartina alterniflora marshes at Oak Island, North Carolina. The mean elevation of the Juncus clumps was 2.18 feet above mean sea level (MSL) and the mean elevation of the Spartina alterniflora was 1.97 feet above MSL. The mean high tide was 2.0 feet above MSL. Adams (personal communication) suggests that these clumps are the remnants of a more extensive Juncus marsh that was invaded by S. alterniflora as the sea level rose.

Kurz and Wagner (1957) found Juncus often entering the surrounding flatwoods (Fig.3) and on the tops of barrier beaches with elevations up to 4 feet. In one flatwood Juncus was found growing with magnolia sprouts. Most of the Juncus, however, is found in relatively pure stands at lower elevations (slightly above mean high tide) and it is this marsh to which the discussion is limited.

Kurz and Wagner (1957) used U. S. Coast and Geodetic Survey tide tables and transects across marshes, correlated with U. S Coast and Geodetic Survey bench marks, to show that a pure stand of Juncus marsh

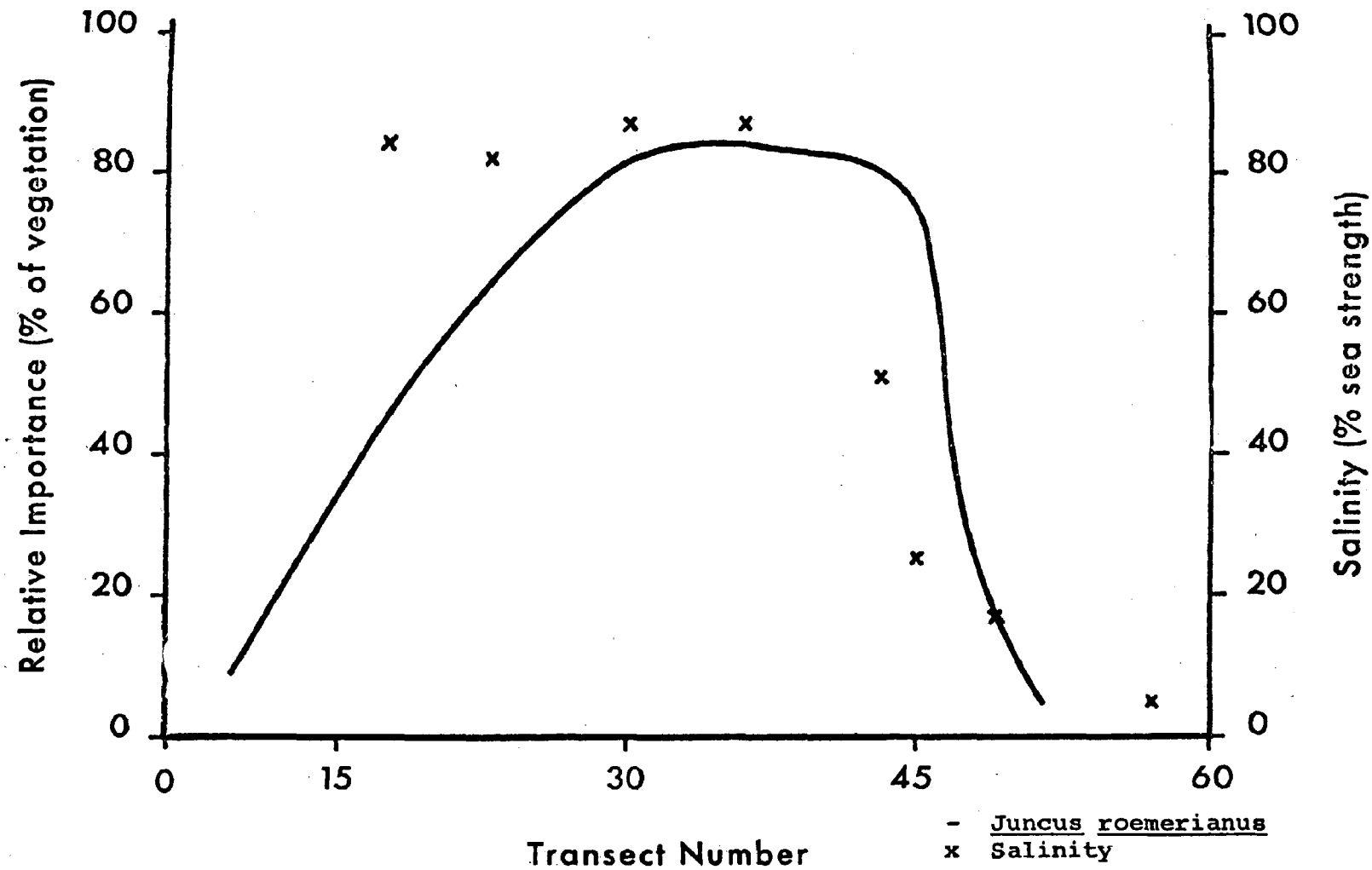

Fig. 7. Relationship between the relative importance of the Juncus roemerianus vegetation type on the Lockwood Folly River and the soil water salinity under needle rush in the middle of the marsh (Foster, 1968).

Table 2. Germination of *J. roemerianus* seeds in varying concentrations of sodium chloride (Seibert, 1969)

Percent sodium chloride	Days until initial germination	Percent germination at end of 72 days
0.0	8	68.9
0.5	11	73.3
1.0	20	37.4
1.5	-	-
2.0	-	-
3.0	-	-

Table 3. Germination of *J. roemerianus* seeds in varying concentrations of sodium chloride and sea water (Seibert, 1969)

Percent salinity	Sodium chloride	Sea water	
	Percent germination after 21 days	Percent germination after 21 days	Percent germination in distilled water
0.0	90.0	78.0	-
0.5	21.0	20.0	82.1[a]
1.0	-	-	75.3
1.5	-	-	92.0
2.0	-	-	88.0
3.0	-	-	89.3

[a]These include only the seeds from the sea water experiment which were ungerminated at the end of 21 days.

in northwest Florida was 3.24 feet above mean low water (MLW) and to predict that this elevation would be covered by water 81 times per year. Stalter (1968), using a recording tide gauge correlated with marsh transects, found a Juncus marsh in South Carolina inundated an average of 60 minutes per day. Waits (1967), using similar measurements reported large pure stands of Juncus marsh at 1.62 feet above MSL and the average high tide to be only 1.2 feet above MSL.

Juncus Morphology and Growth Patterns

Foster (1967) states that Juncus reproduces vegetatively by means of underground rhizomes (Fig.8). "Each shoot which bears the emergent leaves is a short, non-elongated stem located below the soil surface.... The main leaves are terete, slender, and erect with sharply pointed apices. New leaves are produced at the apex of the shoot so that the base of the youngest leaf is enclosed by the sheathing leaf base of the next youngest leaf. Leaves are generally 0.5 to 2.0 meters tall and vary in numbers from one to six or more per shoot...."

"Some of the stems elongate in the spring and bear an inflorescence ending the lives of those shoots. In other cases the shoots die without producing an inflorescence." Seibert (1969) reported that Juncus can be grown from seeds, but he was of the opinion that the plant usually reproduces vegetatively.

Seasonal Patterns

Although Juncus grows and produces new leaves throughout the year (Table 4), Foster (1968) found there was a decrease in the standing crop during the winter (Fig. 9).

MARSH ANIMALS

The numbers and varieties of animals in Juncus marshes are small. Kuenzler (1961) found populations of the mussel, Modiolus demissus in Juncus marsh in Georgia. I have observed mussels in Juncus marsh along the edges of tidal creeks in North Carolina, but have not noticed them in the pure Juncus stands away from the creeks. Davis and Gray (1966) reported relatively low insect population densities in Juncus marsh. Only four species of adult insects were Juncus feeders and only one larval species

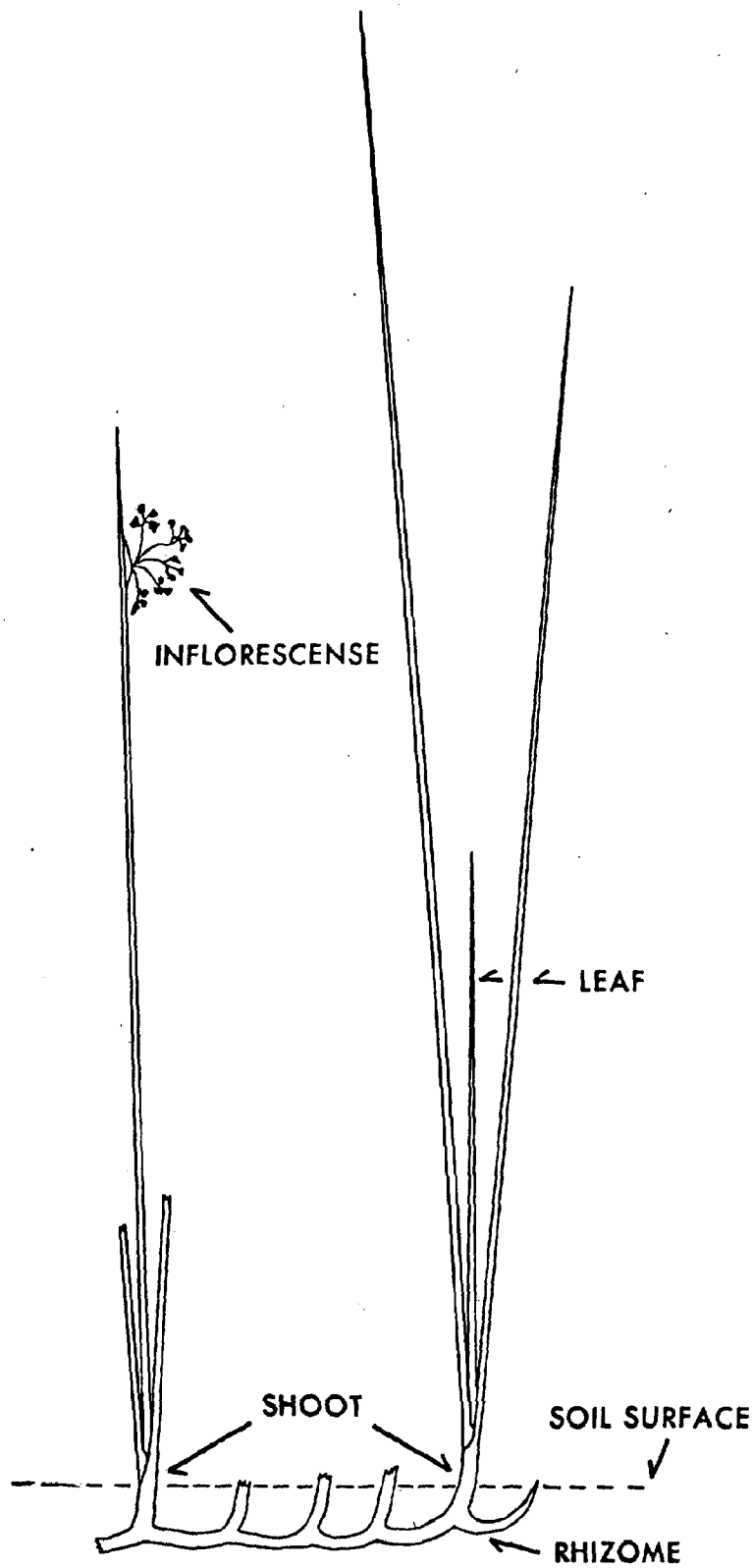

Fig. 8. General morphology of Juncus or needle rush (Foster, 1968).

Table 4. Production of new leaves at existing shoots in growth plots (leaves/100 shoots/28 days) (Foster, 1968).

Period	New Leaves	Period	New leaves
Mar 24		Oct 23	
	18.8		5.5
May 14		Nov 13	
	12.5		4.0
June 4		Dec 11	
	21.2		1.0
July 2		Jan 24	
	10.9		4.9
July 31		Feb 25	
	8.9		15.4
Aug 28		Mar 23	
	15.1		8.8
Sept 25		Apr 15	
	9.6		10.3
Oct 23		May 6	

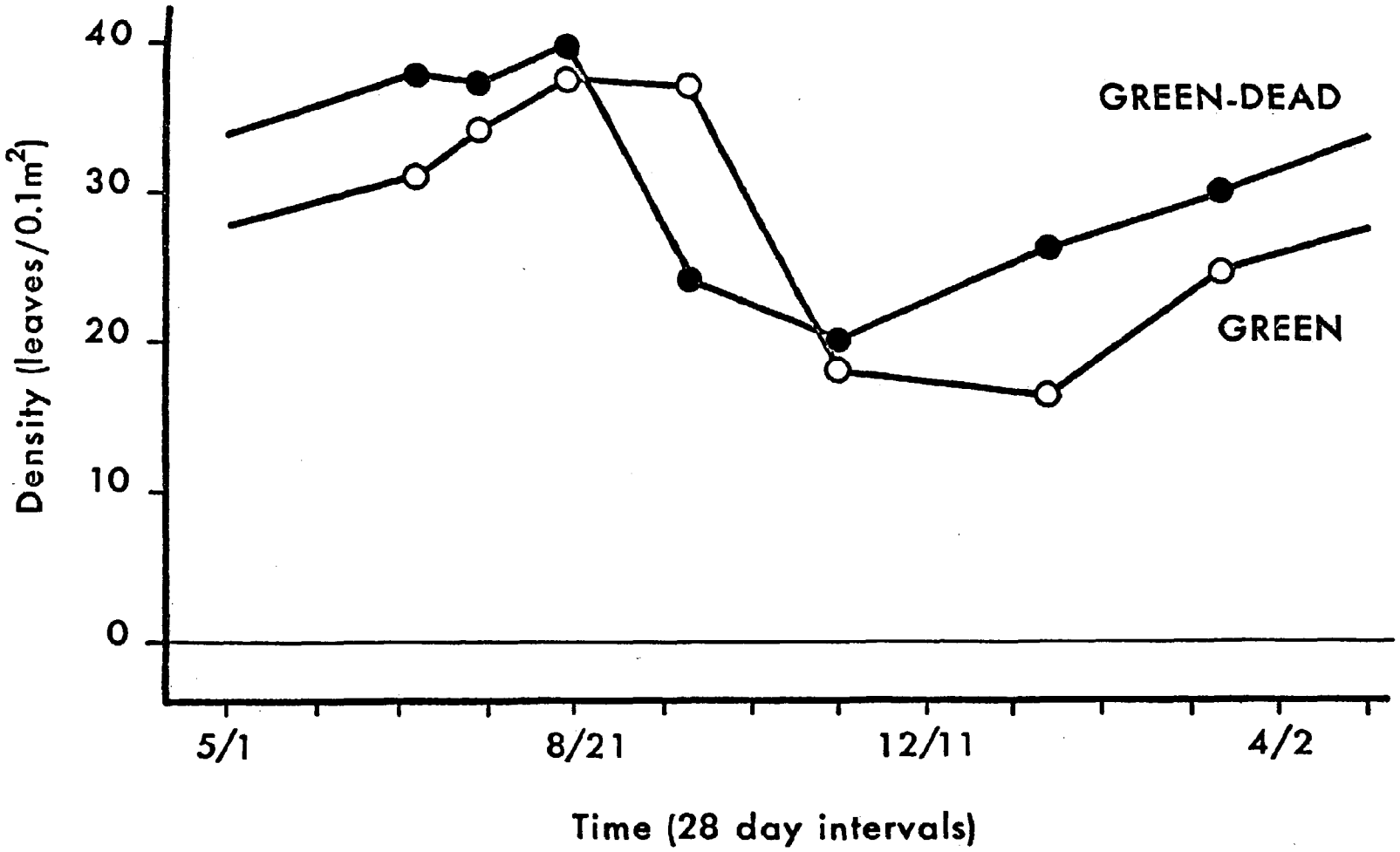

Fig. 9. Mean density of green and green-dead leaves in clip plots (Foster, 1968).

Table 5. Net primary productivity of *Juncus roemerianus* marshes.

Investigator	Productivity/ meter^2/year		Method
	Grams	Kcal.	
Waits (1967)*	1361	6123	Changes in observed living and dead standing crop.
Williams and Murdoch (1968)	735	----	"Compartmental model" Transfer of living crop between categories.
Foster (1968)	560	----	Rates of growth and death of leaves.
Foster (1968)	1006	----	Rates of transfer of leaves between categories.
Stroud and Cooper (1968)	1212	5346	Changes in both predicted living and dead standing crop.

* Averages of data from two years.

burrowed within the tissues. They suggested that the reason for low insect population densities is that the vegetation stands consist of slender, fibrous stems that provide little protection from predators or winds and a scant food supply for primary consumers. Penfound (1952) states that the Spartina-Distichlis-Juncus association in brackish marshes in Louisiana is famous for the production of muskrats.

PRIMARY PRODUCTIVITY

All studies of primary productivity in Juncus marshes have been limited to North Carolina. The more significant studies are summarized in Table 5.

Accurate primary productivity measurements in Juncus are difficult because Juncus leaves are produced all during the year and the seasonal death rate of the leaves varies. Foster (1968) has discussed these problems in some detail. Stroud and Cooper (1968) discussed methods used by different investigators to deal with these problems. Teal (1962) found that Spartina alterniflora marsh (he combined short, medium and tall) at Sapelo Island, Georgia has a net primary productivity of 1600 grams/meter^2/year (6850 Kcal./meter^2/year). Obviously, Juncus marsh is not as productive as Spartina alterniflora marsh, but its productivity is not inconsequential.

RELATION OF JUNCUS MARSH TO THE ESTUARY

The role that Juncus roemerianus plays in the estuarine ecosystem is unknown. Williams and Murdoch (1966) suggested that there was no significant export of Juncus from the marsh and that Juncus marshes have no role in sustaining animal life in the estuary.

Byron (1968), working at Beaufort, North Carolina, studied the nutrient levels during the ebb and flood tides of a tidal creek which drains an irregularly-flooded marsh. He concluded that forty-one percent of the nitrogen entering the marsh, via the tidal creek was not returned to the estuary. Byron also concluded that the marsh was exporting dissolved organic phosphorus. He provides no data however, as to what extent the marsh had been inundated by the flood tides previous to his ebbtide sampling periods. Waits (1967) suggested that transport of nutrient materials from irregularly-flooded marshes could occur during wind and storm tides. He emphasized the need for additional research.

STRESSES IMPOSED BY MAN

Dredge and fill projects and mosquito-control ditches are the greatest threats to Juncus and other plant species in the irregularly-flooded marshes.

Cooper, in another section of this publication, describes the effects of dredging and filling on regularly flooded salt marshes. Similar comments would apply to irregularly flooded salt marshes. Juncus and other high marsh species are in considerably more danger however, from encroachment by adjacent land owners. Also, state administrators hesitate to promote preservation of marsh that has not been "proven" to be vital and whose ownership is often legally tangled.

Apparently, no significant work has been done on the effects of mosquito control ditches on the irregularly flooded Juncus marshes. Cooper suggests that the increased tidal penetration may increase productivity, but stresses the need for additional research. Teal and Teal (1969) suggest that ditches in Juncus marshes encourage growth of Spartina alterniflora along the edges of the ditches, make the productivity more readily available to aquatic organisms, and provide open water space which is used by waterfowl. Recently, I observed changes in ditched Juncus marshes in North Carolina that indicate that the ditches may have some detrimental effects. Baccaris halimifolia, a woody species characteristic of the edges of the higher marsh elevations and probably with lower rates of productivity, was invading the edges of some of the oldest ditches. Many of the ditches had continuous levees along both edges, caused by the coelescing of adjacent spoil piles and by deposition of waterborne silt along the edges of the ditches. If this trend continues water will be retained on the marshes instead of drained. Miller and Egler (1950) describe similar changes in Connecticut marshes in some detail (Fig. 10).

Juncus roemerianus is a scenic and productive marsh species that is a dominant in many estuarine marshes from Maryland to Texas, yet its relationship to the estuary is quite unknown. Questions regarding its importance to the estuary must be answered soon, for Juncus marsh and other irregularly flooded areas continue to be among the first of the coastal ecosystems to be destroyed by real estate development and "marsh improvement" schemes.

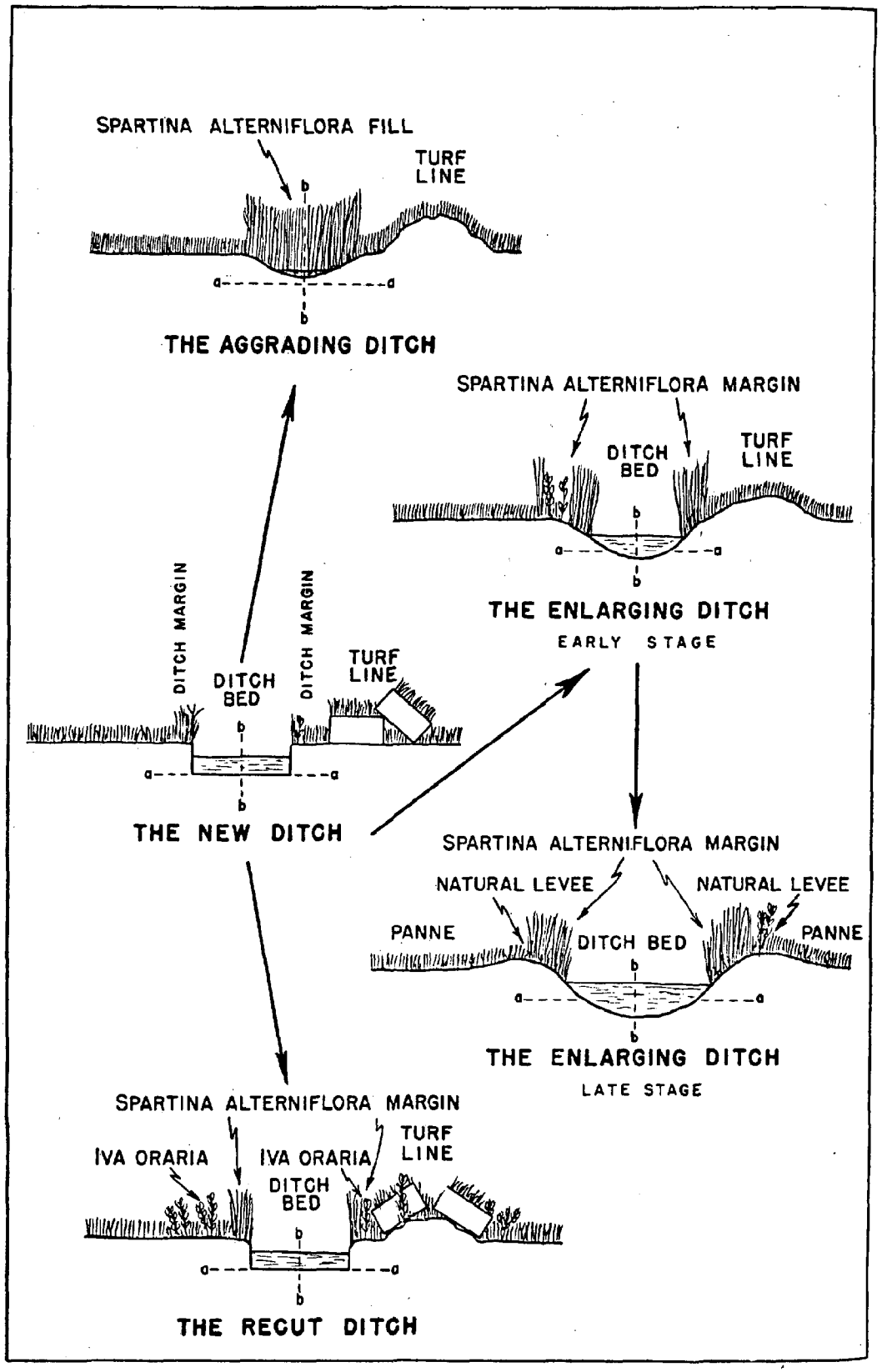

Fig. 10. Diagrammatic cross-section of the mosquito-ditch effects, not drawn to scale. A-A and B-B are the original horizontal bottom and vertical midlines of the ditch (Miller and Egler, 1950).

Chapter C-5

OYSTER REEFS

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One of the dominant estuarine organisms along the Atlantic and Gulf coasts is the common oyster, Crassostrea virginica. In some localities in the southern states, other species of oysters are found in abundance. Along the Pacific coast from Alaska to lower California the native oyster is Ostrea lurida. For economic purposes the common eastern oyster has been introduced to the west coast and to Hawaii, and the Japanese oyster, Crassostrea gigas is grown on the west coast, primarily from imported seed.

Oysters are typically reef organisms growing on their own shell substrate resulting from accumulated generations (Fig. 1 and 2). Intense harvesting and mechanical disturbance of bottoms in estuaries have drastically altered many former natural areas. Reef maps are given in Figs. 3-12.

What is an Oyster Reef?

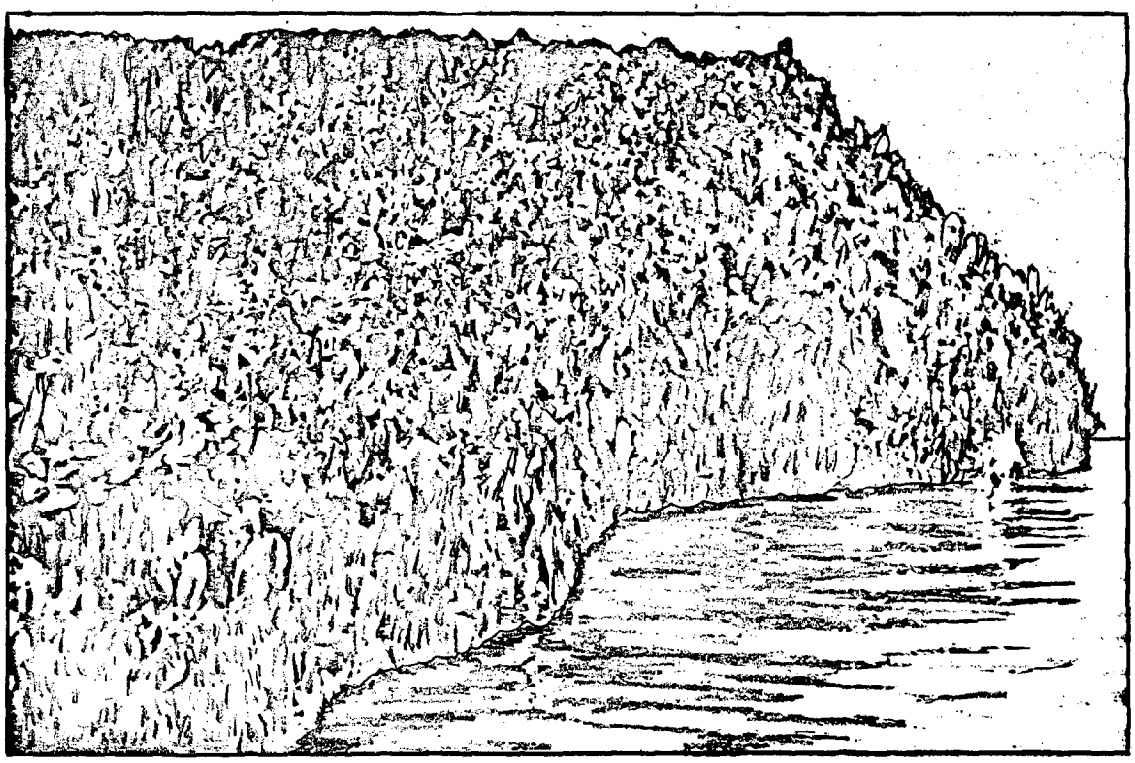
An oyster reef results from the attachment of young oysters during the early stages of the life history to any suitable substrate. A reef may have its beginning from the attachment of a single oyster to any solid material. Succeeding generations of oysters continue to attach to other oysters until a gradual increase in length, width and height takes place in the reef. In shallow waters such development eventually forms a marsh island with a fringe of live oysters in the inter-tidal zone. In deep waters a reef may form a shoal rising several feet above the surrounding bottom (Fig. 3).

Reef development will alter current patterns and velocity, (Fig. 11) change the structure of the bottom and result in an increase and abundance of other organisms to form a distinct community.

A reef developing on soft mud bottom will gradually convert the area into a solid mass of shells and oysters as numbers accumulate (Galtsoff, 1964). Firm bottom may become soft as a result of increase in size of the reef to create a damming effect decreasing the current velocity and forming eddies, thus accelerating sediment deposition (Grave, 1901).

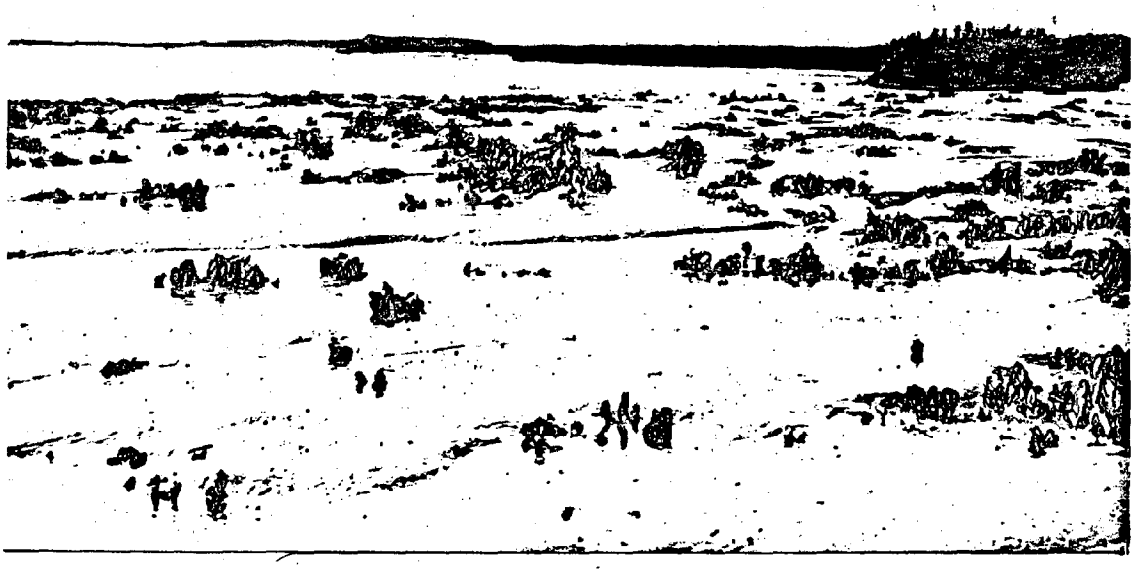
Extensive fossil deposits of oyster shell indicate the enormous size of reefs developed in past ages (Fig. 12). These buried reefs with varying depths of overburden, four to ten feet below the surface and about 25 to 30 feet thick, of varying width and length (one reported 25 miles long and a mile wide), form the basis for a multimillion dollar operation in the Gulf states. Similar reefs are known along the Atlantic coast and some limited dredging is active in the Chesapeake Bay area.

Examination of these fossil reefs show a variety of associated animal forms, particularly those with exoskeletons that would be preserved.



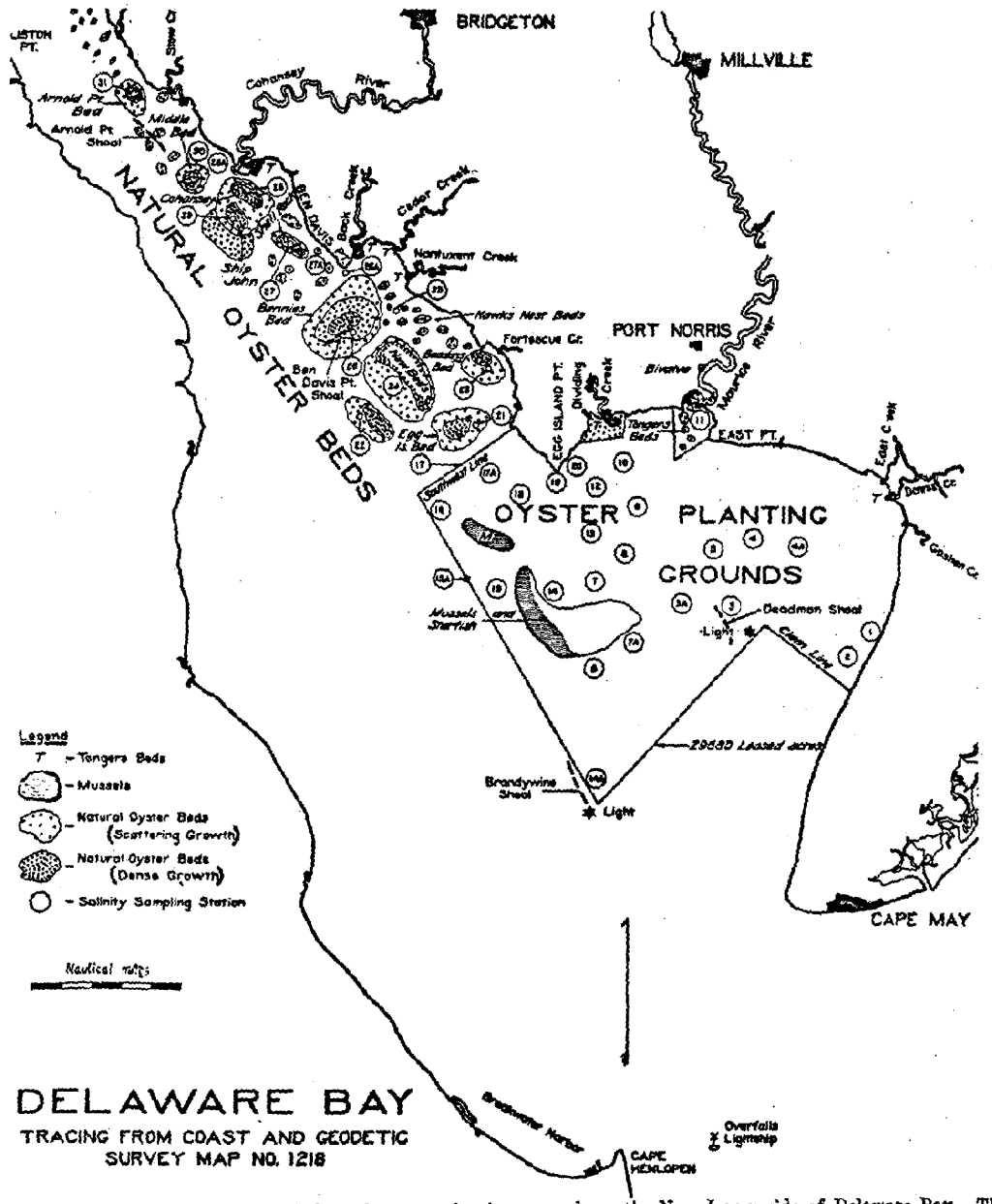
-Oyster reef in Altamaha Sound, Ga., at low tide, March 1925. The highest point was about 6 feet above the bottom; water at the foot of the reef was 8 inches deep. The reef consists of live oysters growing on the side and upper surfaces and attached to empty shells.

Fig. 1. Sketch of mature oyster reef based on photograph from Galtsoff (1964).



—Initial stage in the formation of an oyster bank on very soft mud of a tidal flat. Photographed at low tide near Brunswick, Ga.

Fig. 2. Sketch of young oyster reef based on photograph from Galtsoff (1964).



The natural oyster beds and oyster planting grounds on the New Jersey side of Delaware Bay. The Cape May flats referred to in this paper are located at 2 within the circle. (From T. C. Nelson, exhibits submitted with testimony, Delaware Diversion Case, U. S. Supreme Court, 1929. Reprinted in Perkins, E. B. 1931 "Story of an Oyster." N. J. State Bd. of Shellfisheries.)

Fig. 3. Oyster reefs in Delaware Bay (Nelson, 1947).

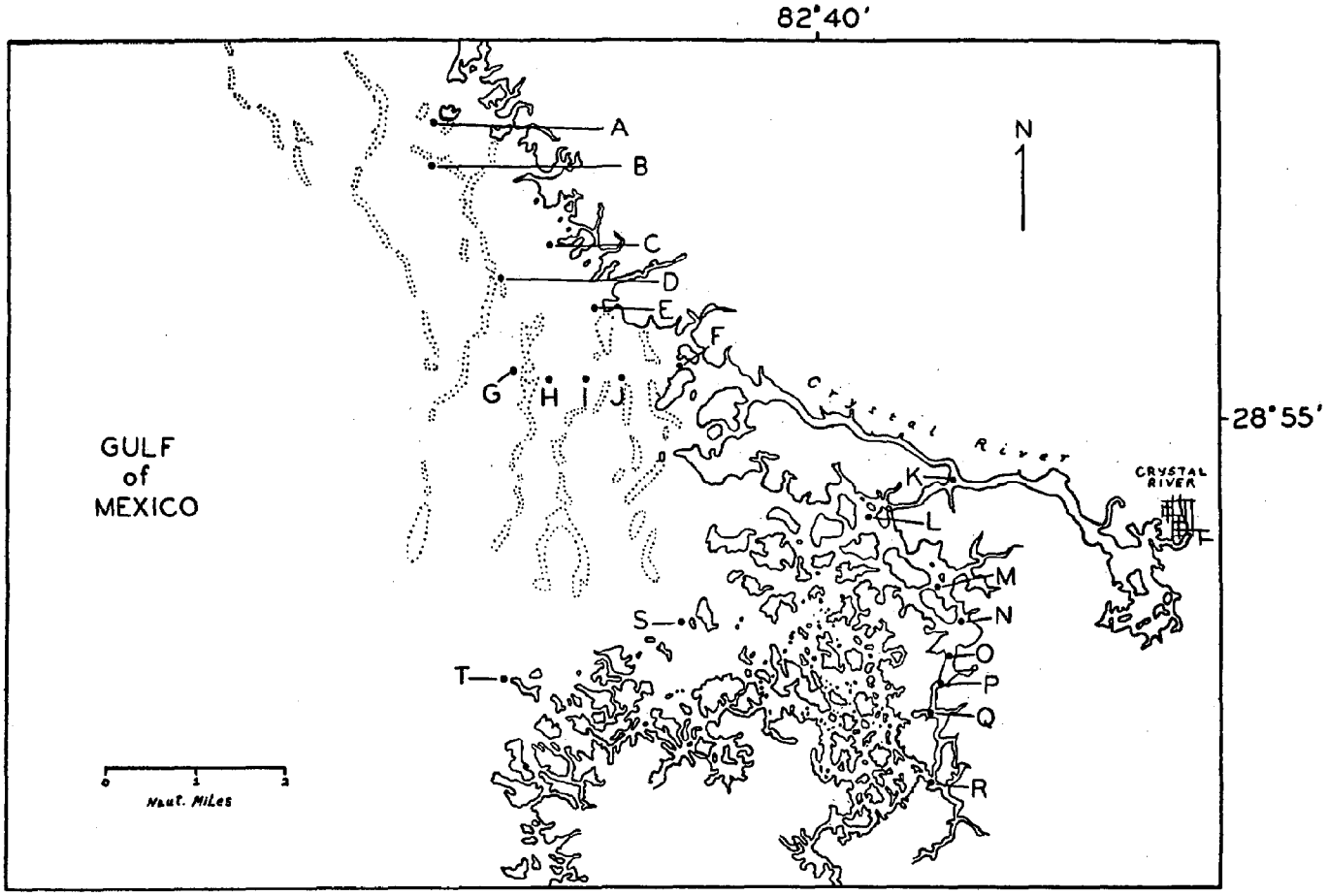
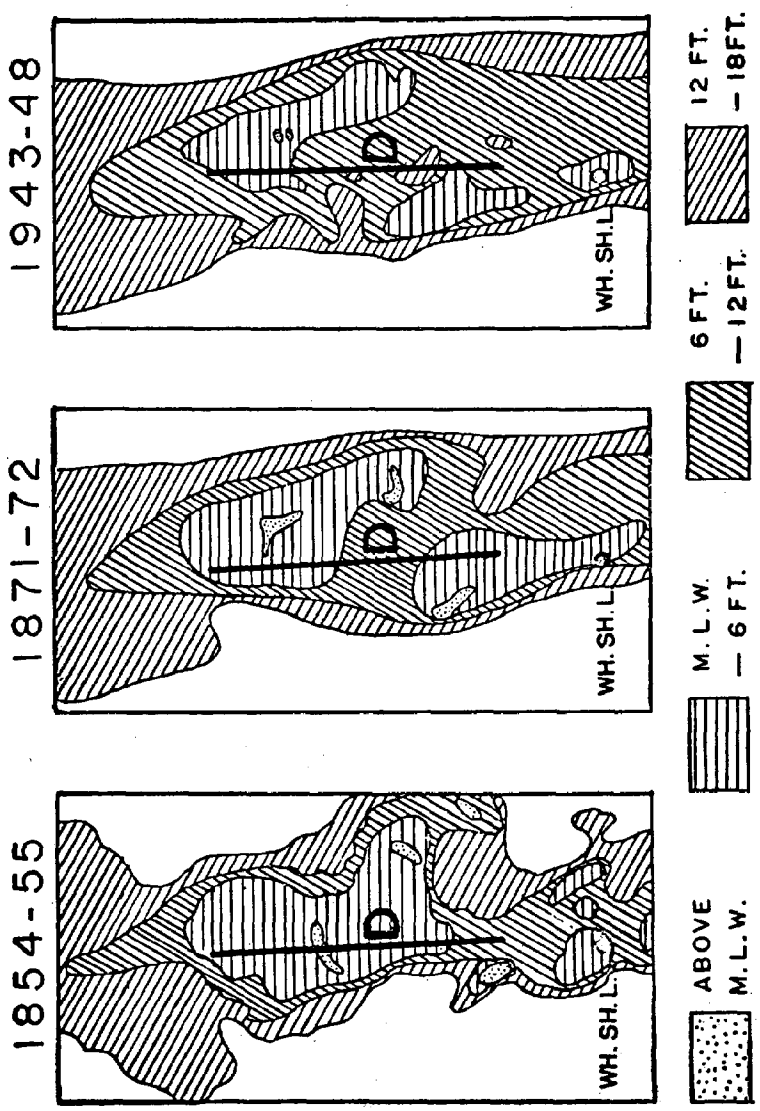


Chart of the Crystal River area showing survey stations and general location of offshore reefs. Letter key for stations as follows: *A*—Drum Island; *B*—Demory Gap; *C*—Negro Island; *D*—Tin Pan Gap; *E*—Black Point; *F*—Shell Island; *G*—Mkr. #5; *H*—Mkr. # 10; *I*—Mkr. # 12; *J*—Mkr. #16; *K*—Salt River Branch; *L*—Big Coon Gap; *M*—Lewis Creek; *N*—N. Dixie Bay; *O*—S. Dixie Bay; *P*—N. Narrows; *Q*—Mid Narrows; *R*—S. Narrows; *S*—Mullet Key; *T*—Mangrove Point.

Fig. 4. Oyster reefs on the west coast of Florida in an estuary fed by hard clear spring-waters (Dawson, 1955).



Depth Contours in the Vicinity of White Shoals Light. Traverse D, 1000 yards, is drawn in to show location and scale.

Fig. 5. Oyster bars in the James River estuary of Virginia (Marshall, 1954a).

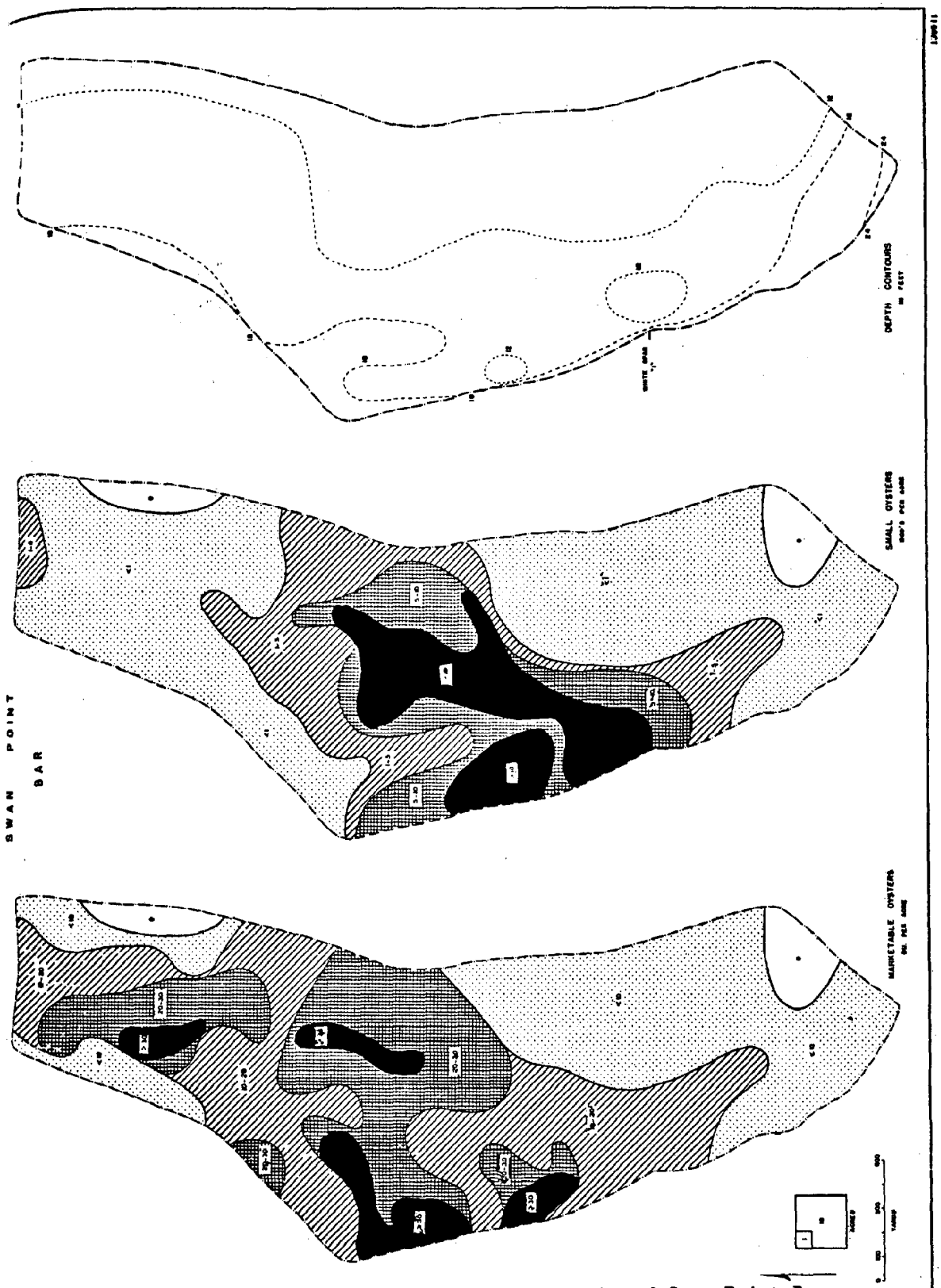
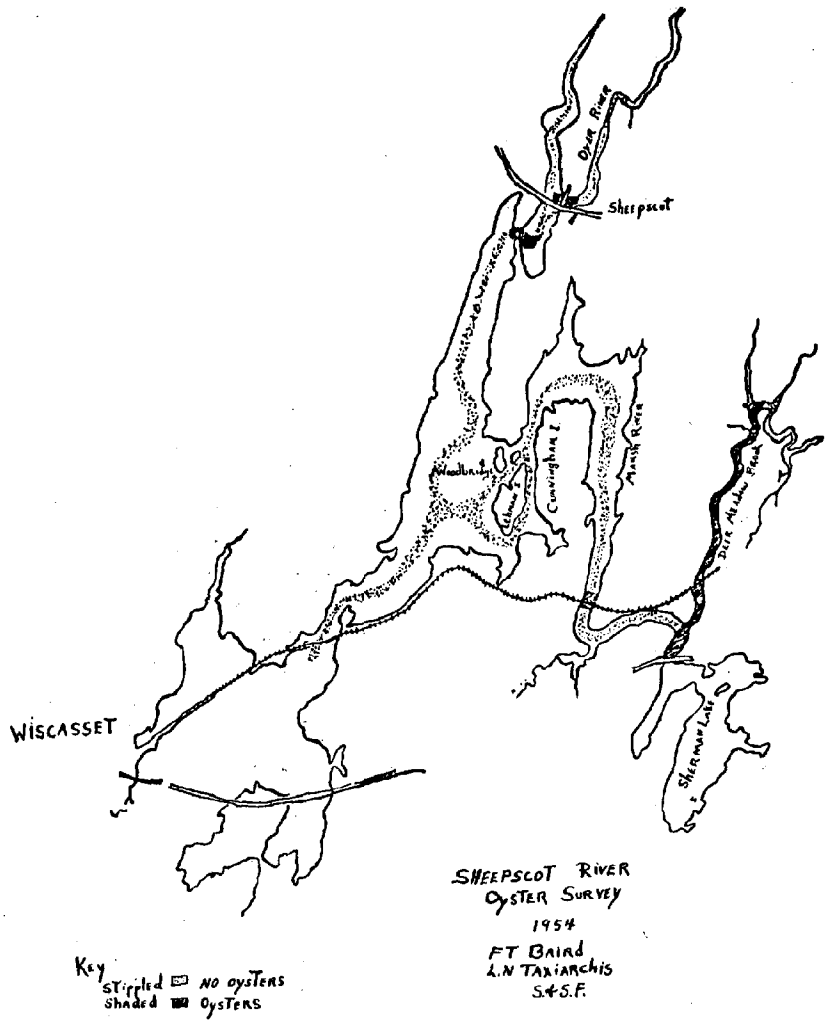


Fig. 6. Oyster bars of the Potomac River (Frey, 1946).



From the pool above Sheepscot Dam drags were made up the east channel which passes under the Sheepscot Bridge and swings east into the Dyer River under the small bridge. Drags were taken along the Dyer to a point where the river makes a turn. Further progress up river was prevented by shallow water. No oysters were found above the mouth of the Dyer.

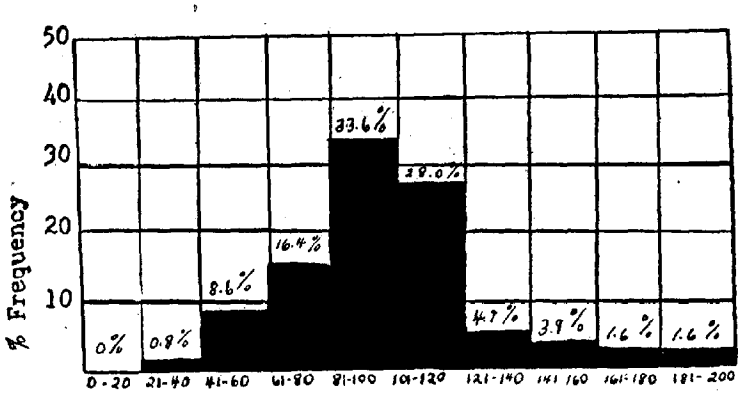


Fig. 7. Oyster beds in the Sheepscot Estuary of Maine (Taxiarchis, Dow, and Baird, 1954).

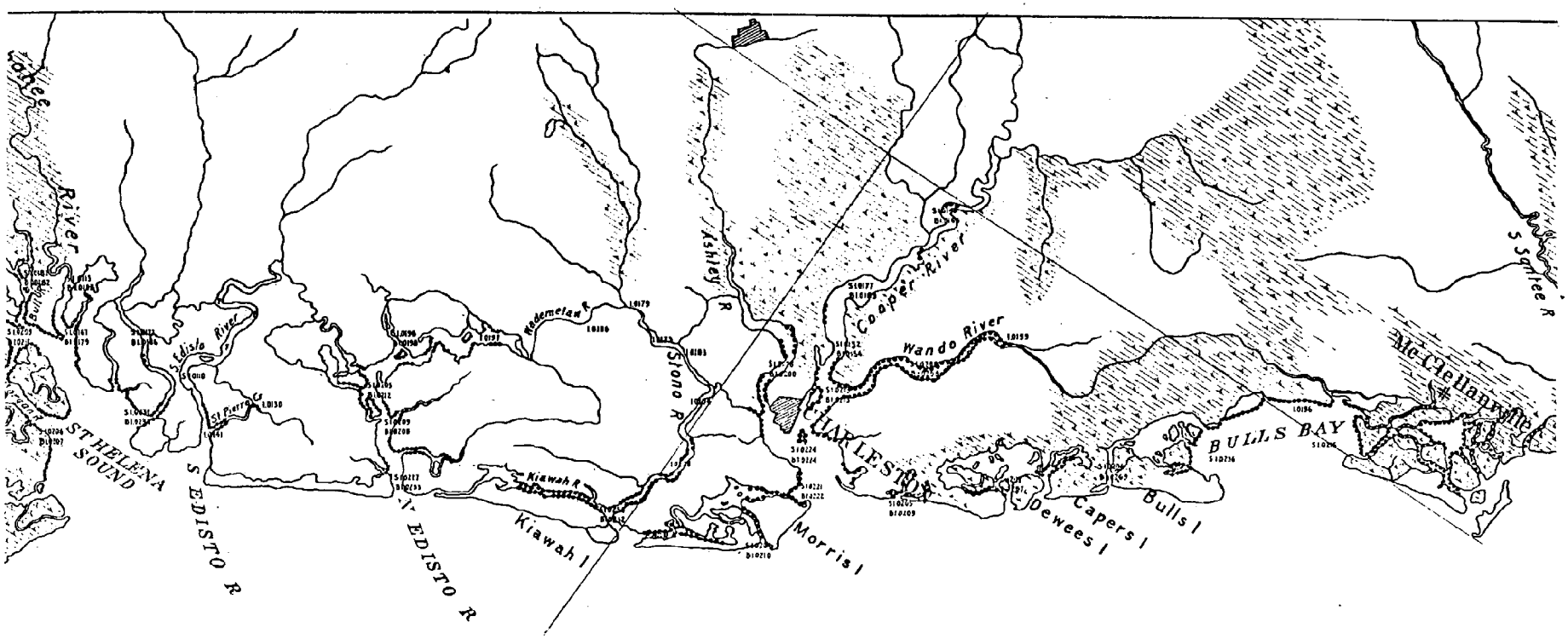
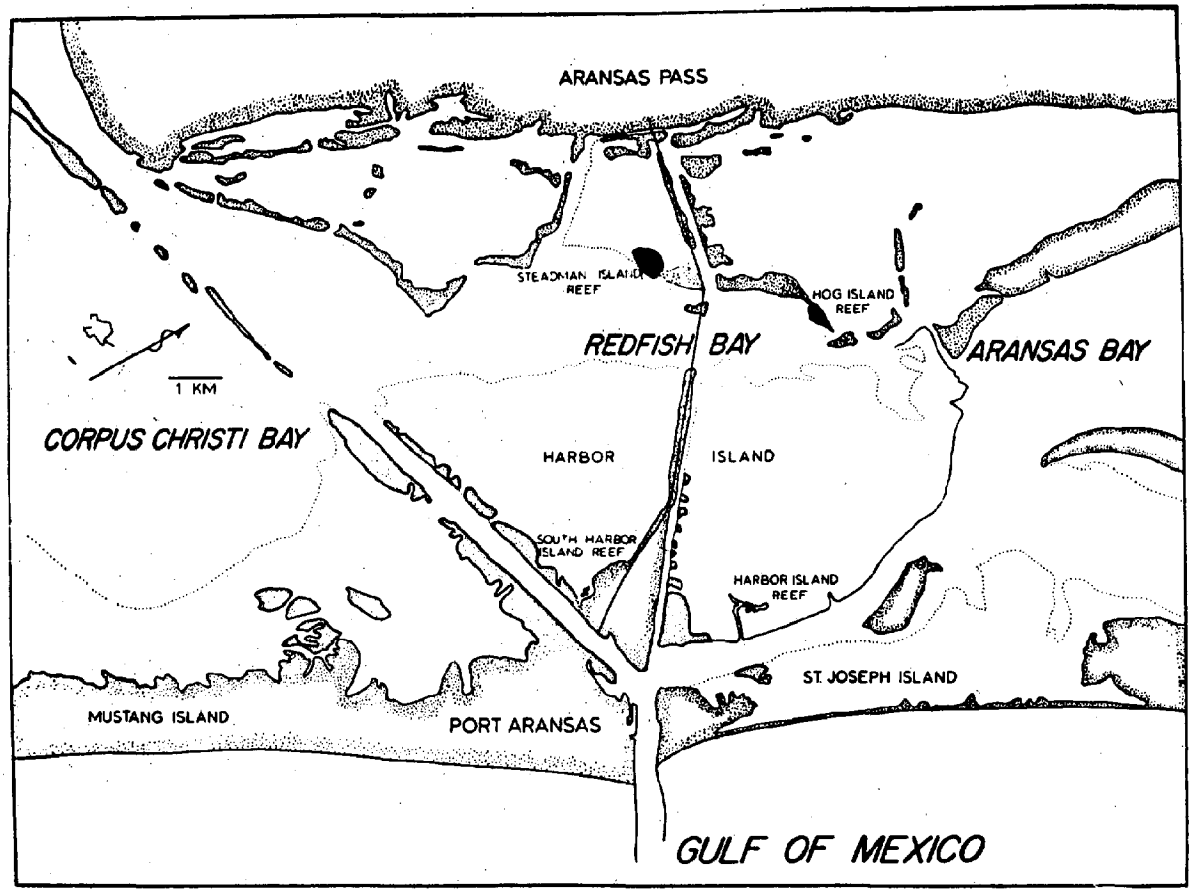
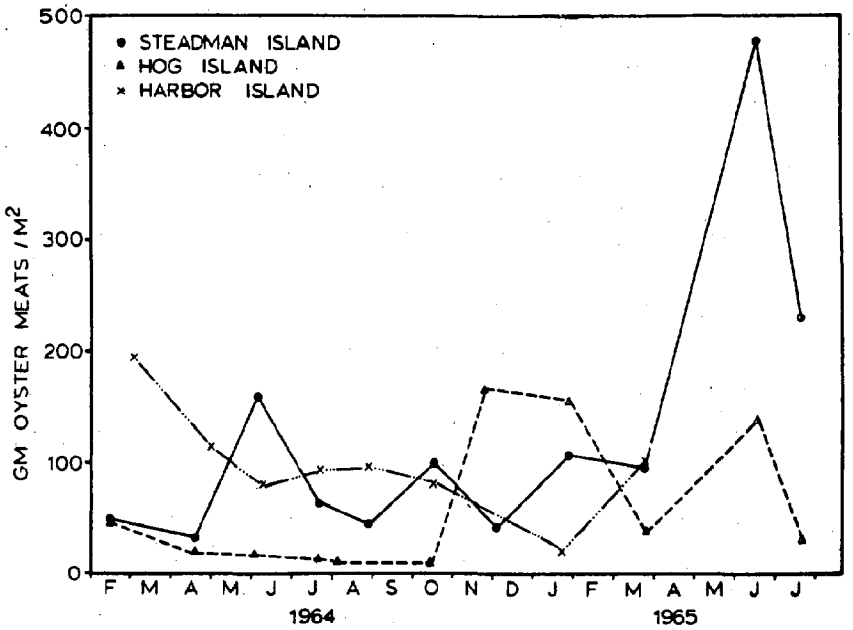


Fig. 8. Oyster reefs in South Carolina (Galtsoff and Prytherch, 1927).

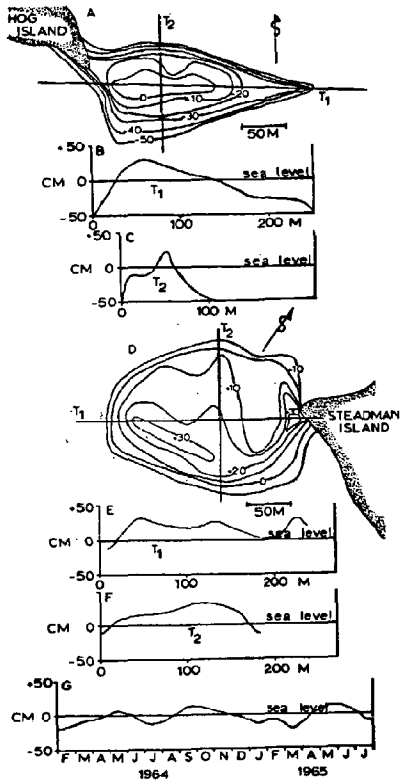


A diagram of the Redfish Bay area of the Central Texas coast. The arrow indicates the relative area on the Texas coast. The four reefs considered in this study are indicated in black.



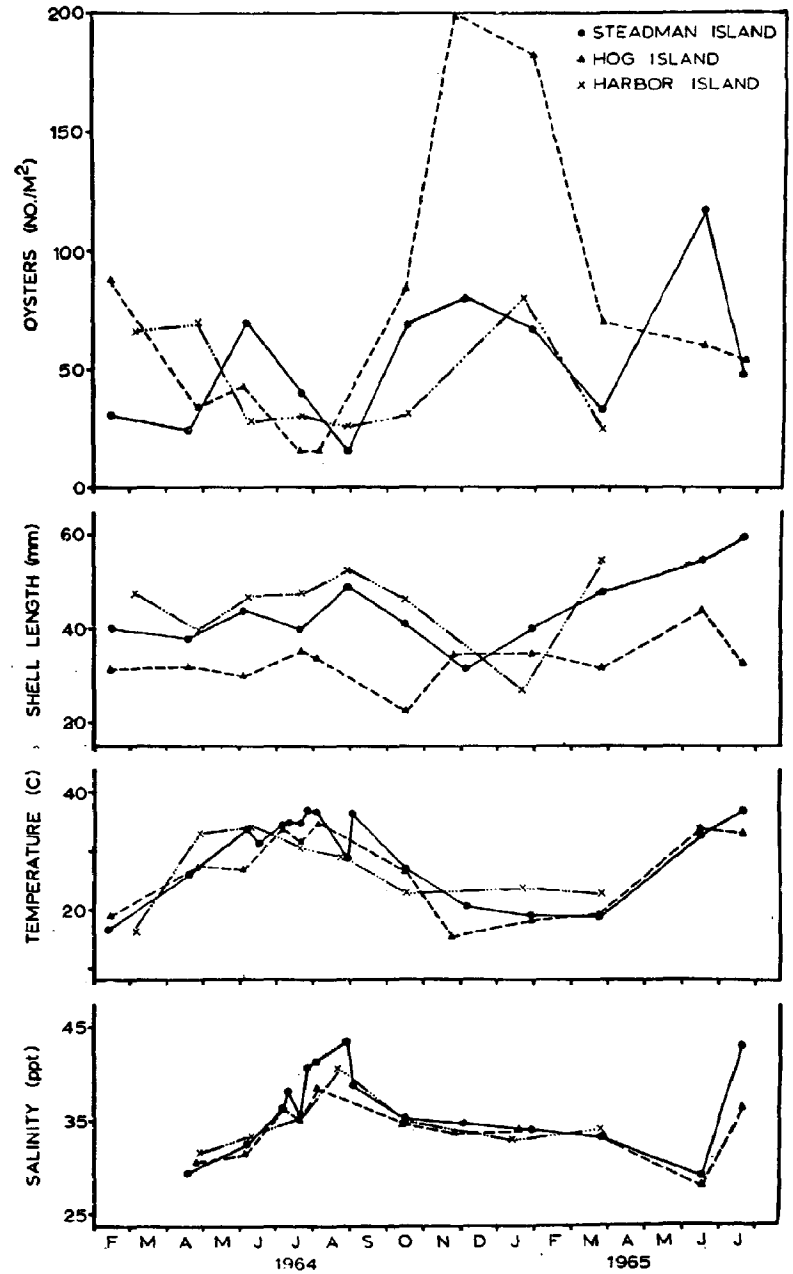
The amount of oyster meat per square meter on each reef during the study period. Each point was computed by multiplying the average meat weight for the average shell length (from Fig. 4) by the average number of oysters per square meter.

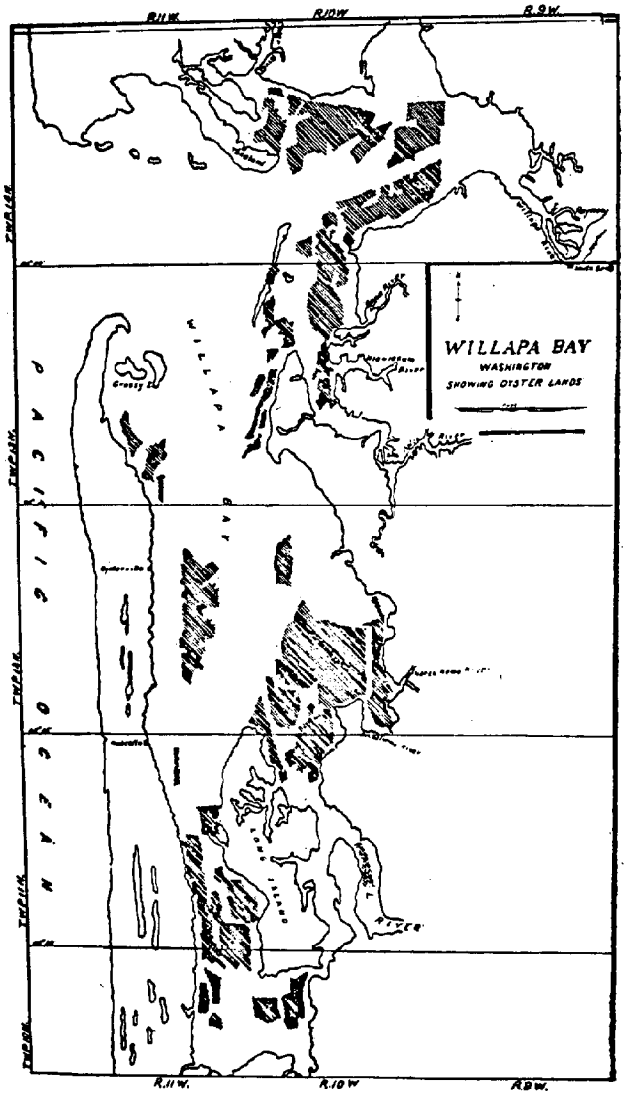
Fig. 9a. Intertidal oyster reefs in Texas (Copeland and Hoese, 1966).

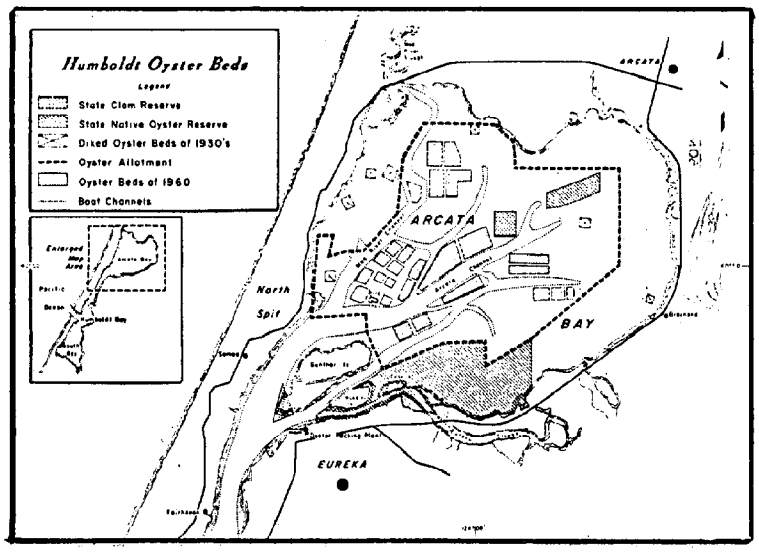


Profiles of the two major reefs and mean water level during the study period. The horizontal line labeled sea level on each graph represents *mean* sea level as based on U.S. Coast and Geodetic Survey Markers. A. Contour drawing of Hog Island reef. Each contour is ten cm higher than the one just outside it. The zero contour is mean sea level; B. A profile along the length of Hog Island reef (T_1); C. A profile across Hog Island reef (T_2); D. Contour drawing of Steadman Island reef. Each contour is ten cm higher than the one just outside it. The zero contour is mean sea level; E. A profile along the length of Steadman Island reef (T_1); F. A profile across Steadman Island reef (T_2); G. Mean monthly water level in Aransas Bay (adjacent to Redfish Bay) during the study period. Each monthly level is the mean of daily values. (These data are courtesy of U. S. Coast and Geodetic Survey, Washington, D. C., Mrs. Martha A. Winn).

Fig. 9b. Intertidal oyster reefs in Texas (Copeland and Hoese, 1966).







Northern Humboldt Bay oyster beds.

Fig. 10. Managed oyster plantings of the west coast. above, Willapa Bay, Washington(Kincaid, 1951); below Humboldt Bay, California (Barrett, 1963).

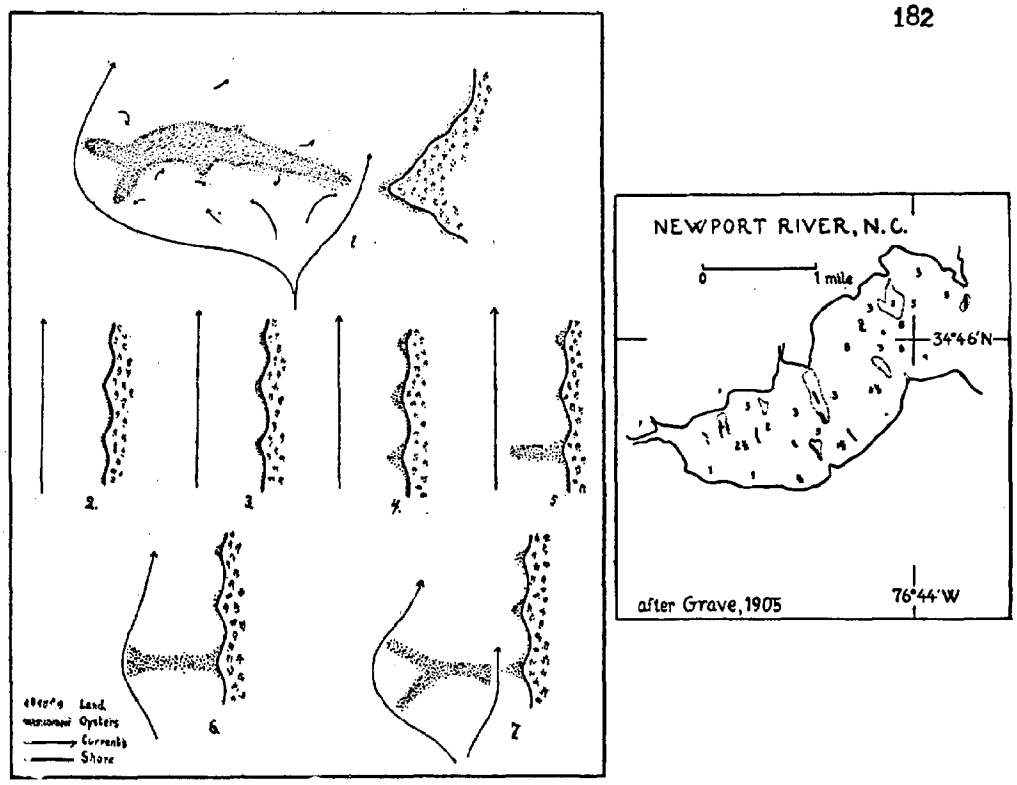
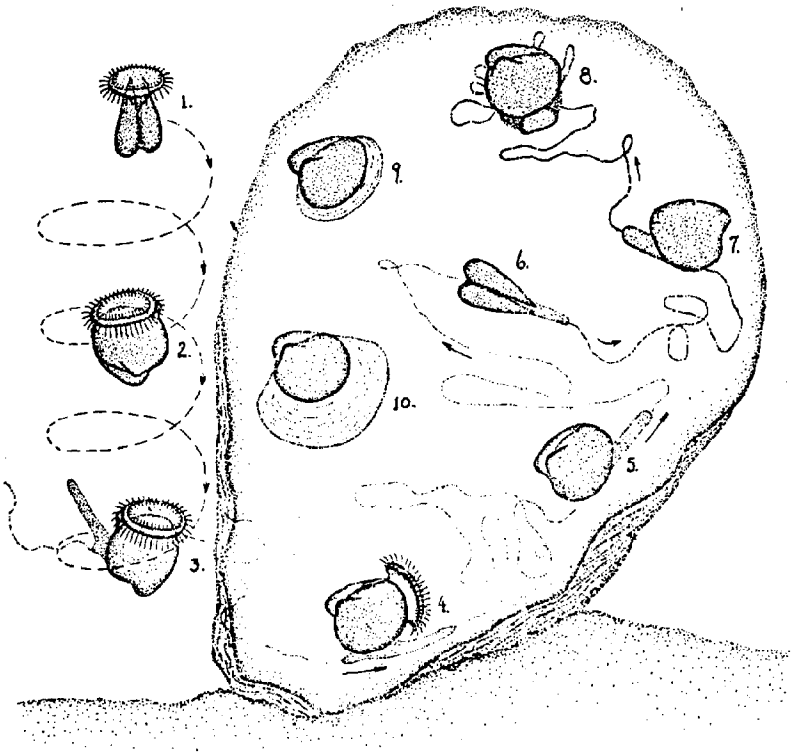


Fig. 11. Configurations of oyster reef development in North Carolina (Grave, 1901).



The setting process (diagrammatic, proportionate size of larvae greatly increased). 1 and 2, swimming larvae, side and end views; 3 and 4, searching phase; 5 and 7, crawling phase; 8, fixation to substratum; 9 and 10, spat one and two days old.

Fig. 12A. Oyster larvae in process of settling and metamorphosis (Prytherch, 1934).

Sketch of an oyster clump from South Bay, near Port Isabel. Animals represented include the anemone, *Aiptasia pallida;* the brittlestar, *Ophiothrix angulata;* the cucumber, *Thyonacta sabanallensis;* a chiton, *Ischnochiton papillosus; Brachidontes exustus, Crepidula fornicata,* and *Anachis avara,* various worms, barnacles, and a small xanthid crab.

Fig. 12b. Oyster associations (Hedgepeth, 1953).

Reef Community

Examination of oyster reefs and bottoms throughout the world show an abundance of forms associated with the oyster. A single shell or live oyster frequently contains a myriad of attached and free living micro and macrofauna (Table 1-2).

A reef affords solid substrate for organisms that attach and become sedentary. These include many forms of algae, hydroids, bryozoans, barnacles, mussels, tube-building worms and other forms that are considered as epifauna dwelling on the surface. Other forms may be found boring into the shells, such as boring sponges, boring mollusks, perforating algae and burrowing worms. Numerous animal forms find shelter in the crevices that are created with growth of the reef. Various animals that prey upon oysters are attracted to reefs. These include a variety of boring snails, sea-stars, crabs and fishes. See Fig. 13.

The kind and number of species in the community will depend upon environment, temperature, salinity and other factors limiting distribution and growth. Reefs are often found where salinities are highly variable. One example is indicated by Loosanoff (1932) in Fig. 14.

In a natural or undisturbed state an equilibrium can be expected between the oyster and the environment. Since the oyster is a sedentary animal, it is not capable of escaping from enemies nor from drastic changes in natural conditions. Temporary changes can be tolerated for several days by shell closure but in cases where prolonged changes persist the animal will be exposed. Excessive rainfall and flood waters may result in complete mortalities of some reefs. With subsequent increase in salinity, larvae may again attach to restore an oyster community. A record of high set of new larvae by season is given in Fig. 15 from Chesapeake Bay.

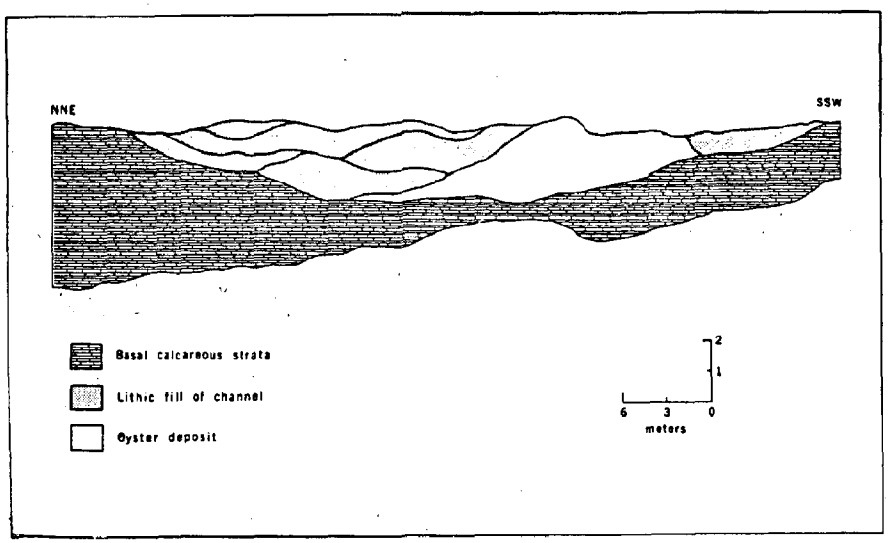
EXAMPLES

Representative of oyster bars in temperate estuaries of the East Coast are the reefs shown for the Delaware (Fig. 3), for west coast of Florida (Fig. 4), for the James River, Virginia(Fig. 5); for the Potomac River (Fig. 6) and Sheepscot estuary of Maine (Fig. 7), tidewaters of South Carolina (Fig. 8) and shoalwater zones of south Texas (Fig. 9). An example on the west coast is Willapa Bay (Fig. 10). For reefs in Pearl Harbor, Hawaii, See **Part I, Volume 1.**

Table 1. COMPOSITION AND CHARACTERISTICS OF THE BEAUFORT, NORTH CAROLINA RECENT MINIMAL OYSTER COMMUNITY*

Taxa	Total Species	Soft-Bodied	With preservable hard parts Ca	Ch	Si	Ph	Possible Redundancy
Porifera	5	—	—	—	5	—	3
Coelenterata	6	5	1	—	—	—	—
Platyhelminthes	1	1	—	—	—	—	—
Nemertea	2	2	—	—	—	—	—
Bryozoa							
Ectoprocta	7	4	3	—	—	—	—
Annelida							
Polychaeta	13	13	—	—	—	—	4
Mollusca							
Gastropoda	9	—	9	—	—	—	1
Pelecypoda	13	—	13	—	—	—	2
Arthropoda							
Crustacea	19	10	4	5	—	—	5
Arachnida (?)	1	1	—	—	—	—	—
Insecta	1	1	—	—	—	—	—
Chordata							
Tunicata	2	2	—	—	—	—	—
Vertebrata	1	—	—	—	—	1	1
Totals	80	39	30	5	5	1	15
Percentages of total community	100	49	38	6	6	1	19

* (data from Wells, 1961) Among the arthropods, only decapod crabs with relatively well-calcified and/or well-tanned exoskeletons have been included with the organisms with hard parts.
Ca = calcareous
Ch = chitinous
Si = siliceous
Ph = phosphatic



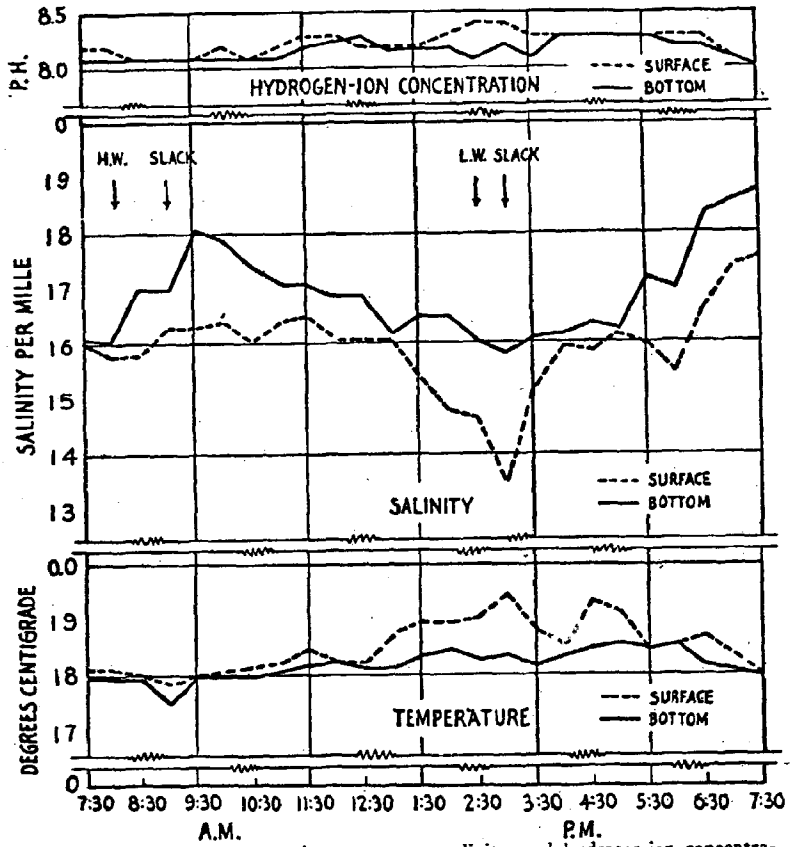
Cross section of the channel deposit at Belgrade, North Carolina. Channel exposed along east side of access road to northwesternmost quarry pit.

Fig. 13. Fossil oyster reef in cross section (Lawrence, 1968).

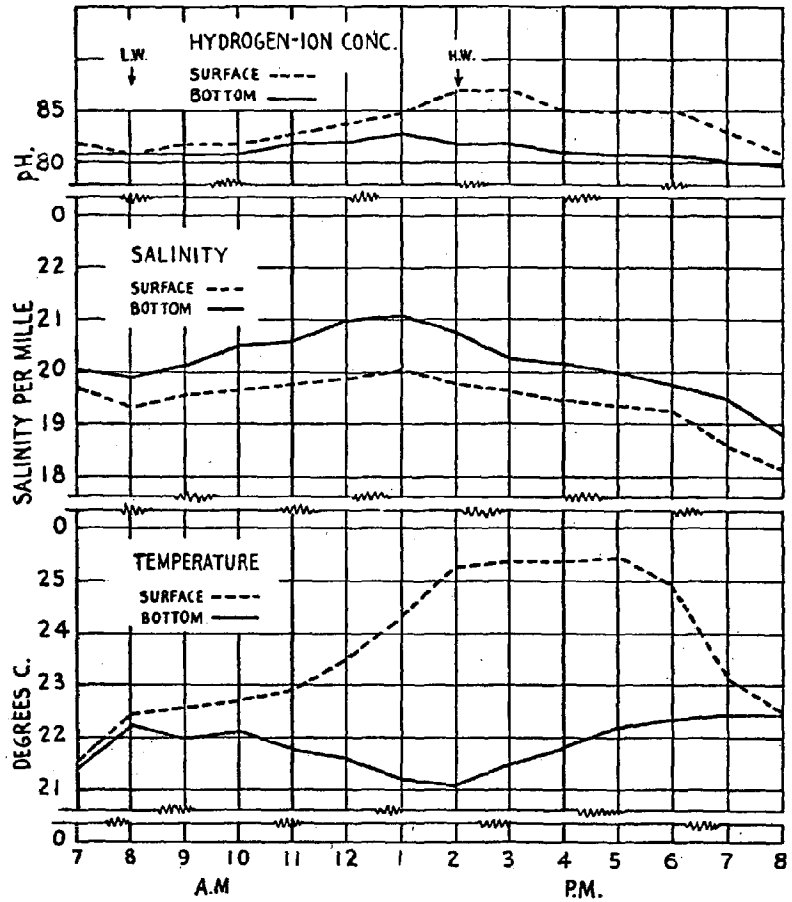
Table 2. Associates of Oysters (Laird, 1961).

Normally free-living organisms recorded from oysters and their immediate vicinity
(C = common, R = rare, X = present, incidence indicated in Tables II and III)

Microorganism (Relevant references follow each name in parentheses)	*O. edulis* St. Andrews, N.B. In mud nearby	*O. edulis* St. Andrews, N.B. On shell	*O. edulis* St. Andrews, N.B. In or on oyster	*O. edulis* Conway, N. Wales On shell	*O. edulis* Conway, N. Wales In or on oyster	*C. virginica* Ellerslie, P.E.I. On shell	*C. virginica* Ellerslie, P.E.I. In or on oyster	*O. belcheri* Karachi, Pakistan On shell	*O. belcheri* Karachi, Pakistan In or on oyster
Bacteria									
Eubacteriales									
Spirillum sp.	C	C	X	—	—	C	X	—	—
Chlamydobacteriales									
Sphaerotilus dichotomus (Cohn) (114)	C	C	X	—	—	—	—	—	—
Protozoa									
Mastigophora									
Euglenoidina									
Anisonema acinus Dujardin (19, 47, 71, 142, 148)	R	R	—	R	—	C	—	—	—
Astasia sp. (71)	R	R	—	—	—	—	—	—	—
Peranema trichophorum (Ehrenberg) (19, 71, 131)	—	—	—	R	—	—	—	—	—
Marsupiogaster picta Faria *et al.* (33, 148)	—	—	—	C	—	—	—	C	—
Tropidoscyphus octocostatus Stein (14, 33, 47, 71, 142)	—	—	—	R	—	—	—	—	—
Dinoflagellata									
Glenodinium foliaceum Stein (19)	R	—	X	—	—	—	—	—	—
Prorocentrum micans Ehrenberg (19, 23, 71, 131)	R	—	X	—	—	—	—	—	—
Protomonadina									
Bodo edax Klebs (19)	C	C	X	—	—	C	X	—	—
Bodo rostratus (Kent) (19, 65, 131, 142)	C	C	X	—	—	C	X	—	—
Monas guttula Ehrenberg (33, 47)	R	—	X	—	—	—	—	—	—
Monas minima Meyer (19)	C	C	X	—	—	C	X	—	—
Oikomonas termo (Ehrenberg) (19, 71, 140)	C	C	—	—	—	C	—	—	—
Rhynchomonas nasuta (Stokes) (33, 47, 90)	C	—	X	—	—	—	—	—	—
Polymastigina									
Dallingeria drysdali Kent (65, 71)	C	—	X	—	—	—	X	—	—
Hexamita inflata Dujardin (16, 17, 19)	R	R	X	—	—	R	X	—	—
Trepomonas agilis Dujardin (19, 71)	R	—	X	—	—	—	—	—	—
Sarcodina									
Amoebina									
Amoeba radiosa Ehrenberg (131, 148)	C	C	X	R	—	—	—	—	—
Ciliata									
Holotricha									
Chilodonella cucullulus (O. F. Müller) (14, 71)	R	C	X	—	—	—	—	—	—
Cinetochilum margaritaceum Perty (62, 71)	—	—	X	—	—	R	—	—	—
Cohnilembus verminus (O. F. Müller) (14, 33, 62, 71, 143)	R	C	X	—	—	C	X	—	—
Colpidium campylum (Stokes) (62)	—	—	X	—	—	—	X	—	—
Colpidium colpoda (Ehrenberg) (14, 113, 143)	—	—	X	—	—	—	X	—	—
Cyclidium glaucoma O. F. Müller (33, 71, 74)	C	C	X	—	—	C	X	—	—
Enchelyodon sp. (16, 17)	—	C	X	—	—	C	X	—	—
Frontonia marina Fabre-Domergue (62, 143, 148)	—	—	—	—	—	R	—	—	—
Lacrymaria coronata Claparède and Lachmann (67, 148)	R	—	—	R	—	—	—	—	—
Lionotus fasciola (Ehrenberg) (14, 33, 62, 71, 74, 143, 148)	R	R	X	—	—	—	—	—	—
Paramecium sp. (71)	C	R	—	—	—	R	—	—	—
Platynematum sociale (Penard) (62)	—	—	—	—	—	—	X	—	—
Pleuronema marinum Dujardin (14, 71, 148)	C	C	X	—	—	C	X	—	—
Urocentrum turbo (O. F. Müller) (62, 71, 74)	—	—	—	—	—	R	X	—	—
Uronema marinum Dujardin (14, 71, 90, 143)	R	R	X	—	—	R	X	—	—
Uronema pluricaudatum Noland	R	R	—	—	—	—	—	—	—
Unidentified tetrahymenids (72, 113)	R	—	X	—	—	—	X	—	—
Spirotricha									
Aspidisca costata (Dujardin) (62, 71, 74)	R	R	X	—	—	C	X	—	—
Condylostoma patens (O. F. Müller) (14, 33, 62, 71, 148)	—	—	—	R	—	—	—	—	—
Euplotes charon (O. F. Müller) (1, 33, 62, 74, 114, 148)	R	C	X	R	—	R	X	C	—
Folliculina sp. (2, 69)	—	—	—	R	—	—	—	R	—
Holosticha kessleri (Wrzesniowski) (14, 62, 71, 148)	—	R	X	R	—	—	—	—	—
Keronopsis rubra (Ehrenberg) (62, 71, 130, 148)	R	—	—	—	—	—	—	R	—
Uronychia setigera Calkins (14, 71)	—	R	—	—	—	R	—	—	—
Uronychia transfuga (O. F. Müller) (33, 71, 143, 148)	—	—	—	—	—	R	X		—
Uronychia sp.	—	—	—	—	—	—	—	R	—
Urostyla gracilis pallida Entz (62)	R	—	X	R	—	R	X	—	—
Peritricha									
Zoothamnium sp. (71)	—	—	—	—	—	R	—	—	—
Suctoria									
Acineta tuberosa foetida Maupas (120, 143)	—	R	X	—	—	—	—	—	—
Sphaerophrya solitiformis Lauterborn (74)	—	—	—	—	—	R	—	—	—
Gastrotricha									
gen. et sp. incert.	R	C	X	—	—	C	X	—	—
Rotatoria									
Diplax sp.	—	—	X	—	—	C	X	—	—
Nematoda									
gen. et sp. incert.	C	C	X	—	—	C	—	—	—

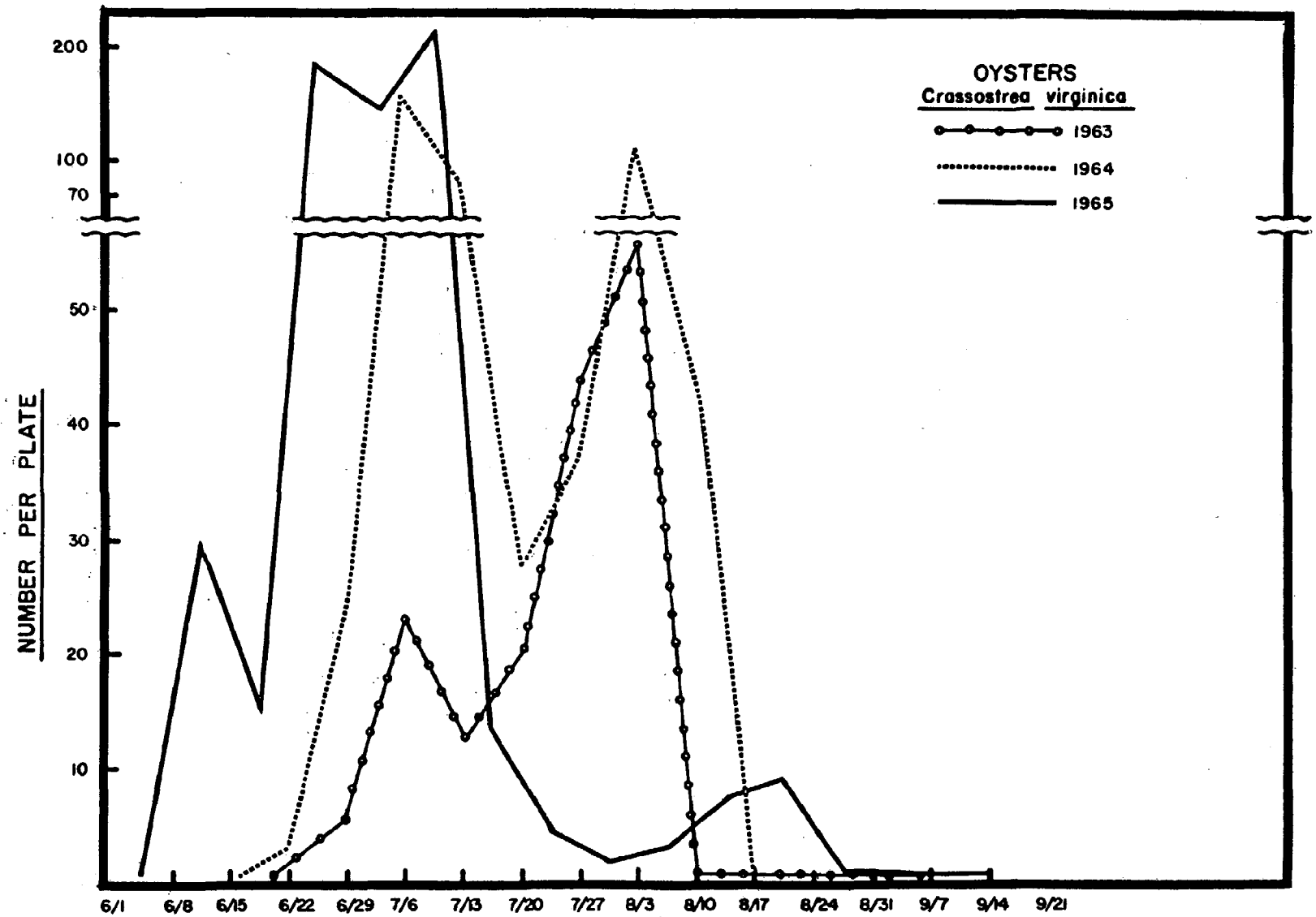


–Half-hourly changes in temperature, salinity, and hydrogen-ion concentration of the water during the tidal cycle at station 3, James River, May 13, 1931.



–Hourly changes in temperature, salinity and hydrogen-ion concentration during a complete tidal cycle on June 4, 1931, Corrotoman River, Va.

Fig. 14. Conditions in the vicinity of reefs (Loosanoff, 1932).



Data for 1963, 1964 and 1965 Showing the Variations in Time of Set from Year to Year in the Chesapeake Waters

Fig. 15. Set of newly attached oysters in Chesapeake Bay (Shaw, 1968).

DISCUSSION

Growth Rates

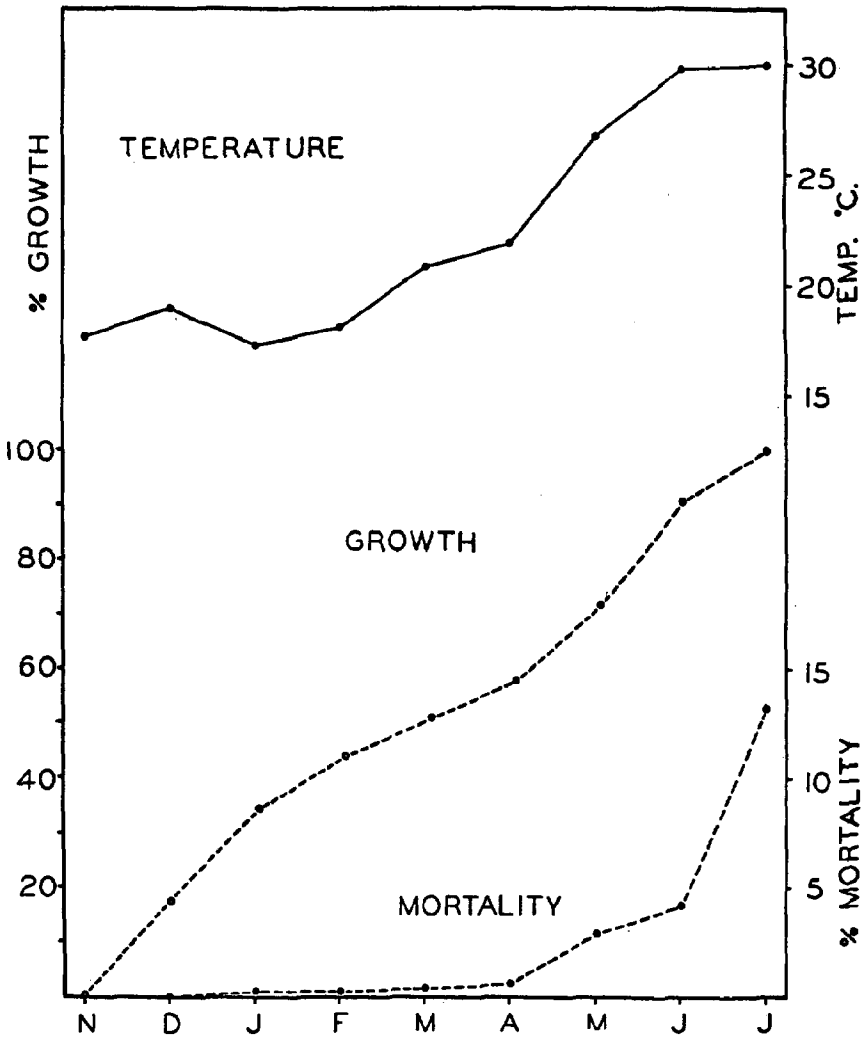
Oysters (Crassostrea virginica) are found growing over a wide range of latitude, from Maine to Florida and Texas and on the Pacific coast and in Hawaii. Water temperatures vary from the freezing point during winter months in the northern areas to highs of over 100° F. in the southern areas.

Temperature influences the rate of water pumping, feeding, reproduction and growth (Galtsoff, P, 1964). The growth period in the northern areas of distribution is limited to the warmer months when temperatures are above 42° F. Further south the growth period may be prolonged throughout the year (Ingle and Dawson, 1952 a and b) (Fig. 16). The growth period in Chesapeake Bay was found to be spread over a seven month period as compared with a five month period at Cape Cod (Shaw, W. N., 1968) (Figs. 17, 18). Continued exposure to high temperature probably reduces the growth rate for ciliary activity and feeding is disrupted. During hot weather in summer months the growth rate has been observed markedly reduced in shallow North Carolina waters. With increasing occurrence of thermal pollution releasing hot water from cooling systems of power plants the relationship of water temperature to oyster growth becomes of interest. In areas of low temperature there may be some beneficial aspects but in other areas there may be adverse results. Temperatures near 40° C are lethal (Fig. 19) although displacement by other organisms may occur at lesser temperatures. Growth of a tropical oyster in Puerto Rico is slower in winter (Fig. 20).

The oysters filter plankton, detritus, and other small particles from the water. Part of the solids go into the digestive tract, some emerging as feces, the rest released as pseudofeces. Depositions show feeding activity (Fig. 21 and Table 4).

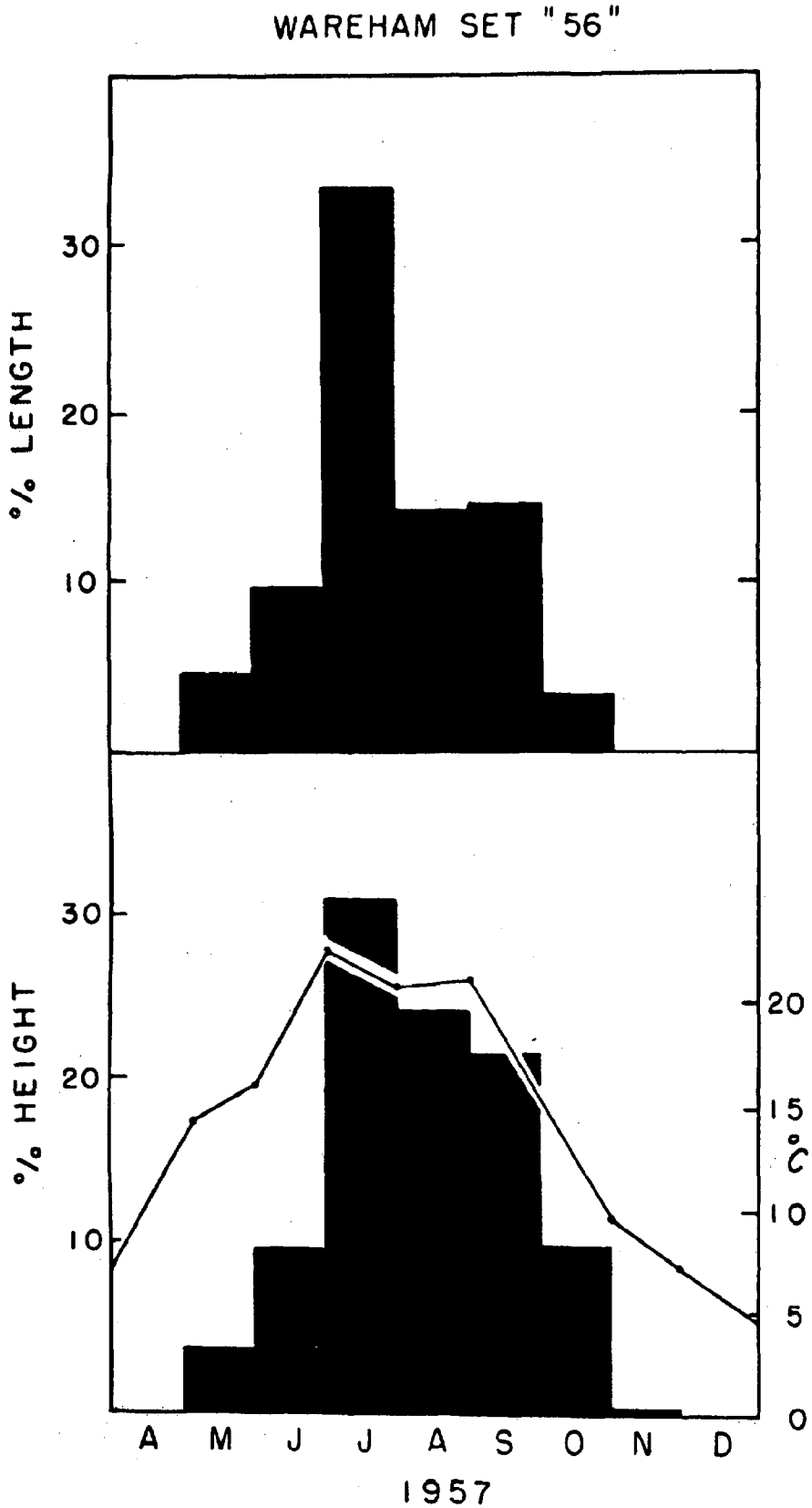
Mortalities

A homogeneous population of animals in concentration, such as a multitude of oysters on a reef, creates a favorable situation for epidemic outbreaks of pathogens and diseases resulting in mass mortalities. Knowledge on oyster diseases has accumulated at a rapid rate in recent years with stimulus from some catastrophic mortalities related to the oyster industry. Recently, in Delaware Bay oyster production dropped from an average above 5 million pounds of shucked meats to 167,000 pounds within 5 years due to disease (Haskin, et al. 1965, 1966). Mortalities have occurred at sporadic intervals. Perhaps the earliest accounts concerning mortalities of the eastern oyster were in the Maritime Provinces about 1915 (Logie, 1956) (Fig. 22). All oyster producing areas are considered as indemic for one or more diseases and disease is probably the greatest cause of mortality (Mackin, 1961b). Environmental factors such as high temperature and high salinities appear favorable to prevalence of some disease forms resulting in higher mortality rates during summer months (Andrews, et al. 1962) (Fig. 23). An excellent review of diseases and parasites causing mortalities in marine mollusks and crustaceans is presented by Sindermann and Rosenfield (1967).



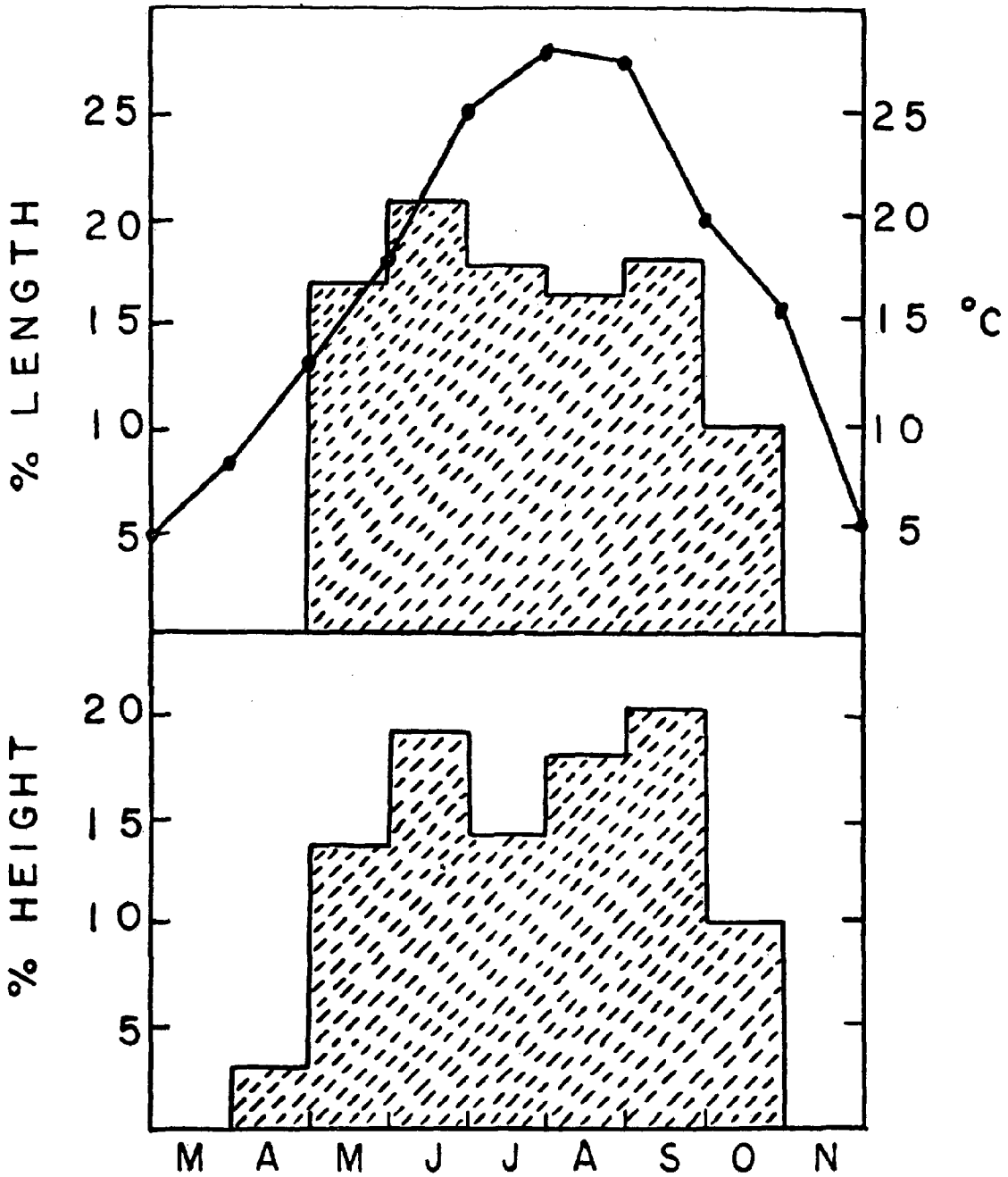
Mean Inverness air temperature, 1951-52; Cumulative per cent growth per month of all experimental oysters, and per cent mortality per month.

Fig. 16. Oyster growth and conditions on the west coast of Florida. See Fig. 4. (Dawson, 1955).



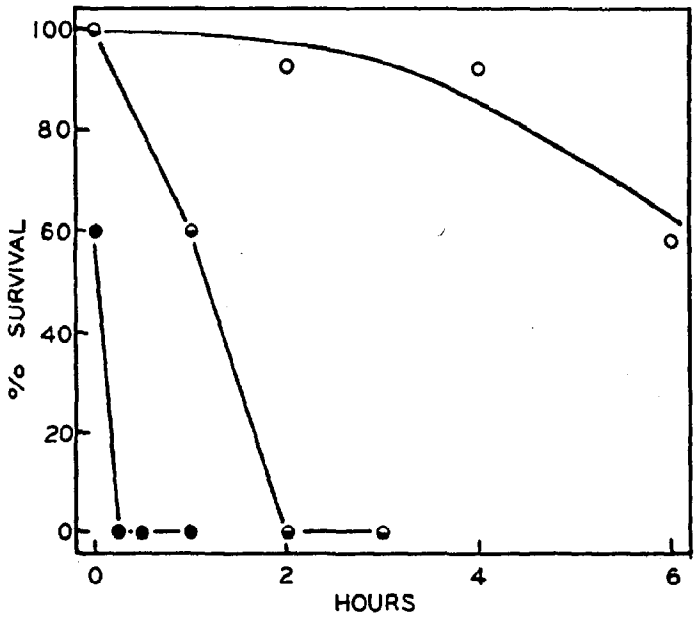
Growth Rate of Oysters Grown at Cape Cod, Massachusetts

Fig. 17. Raft culture of oysters in northern waters (Shaw, 1968).



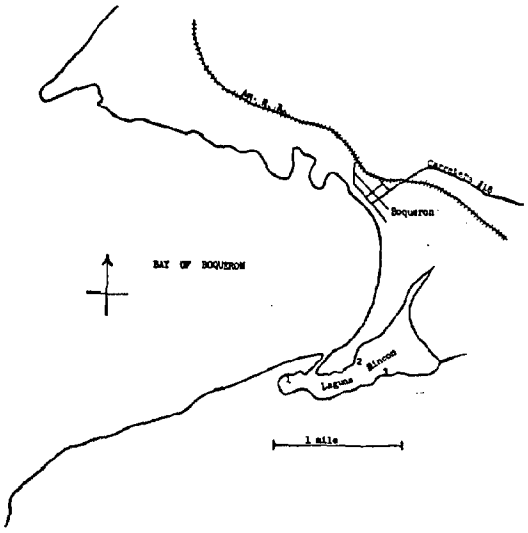
Growth Rate of Oysters Grown at Oxford, Maryland

Fig. 18. Raft culture of oysters in middle Atlantic waters (Shaw, 1968).



Percentage survival at various temperatures during exposure of oysters to constant temperatures of 40°, 42°, and 45° C. Oysters were immersed in water at 24° C and heated at the rate of 4.5° C per hour to the respective test temperatures. Symbols: circles, 40° C; half-filled circles, 42° C; dots, 45° C.

Fig. 19. Oyster survival and temperature



Detailed map of the area at Boqueron Bay showing the lagoon, "Laguna Rincón," where this study was carried on.

Fig. 20a. A tropical lagoon in western Puerto Rico with a population of tropical oysters(Ostrea rhizophrae Gúilding) (Mattox, 1949). Introduction of Crassostrea here did not succeed.

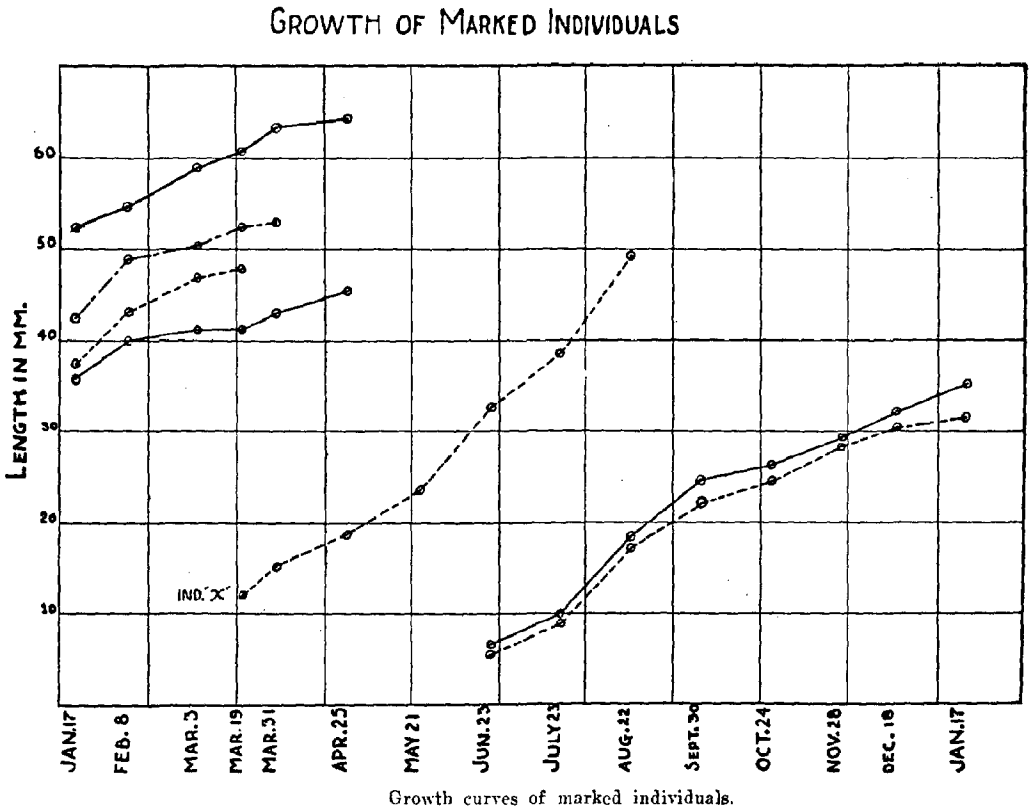


Fig. 20b. Growth of Ostrea rhizophrae (Mattox, 1949).

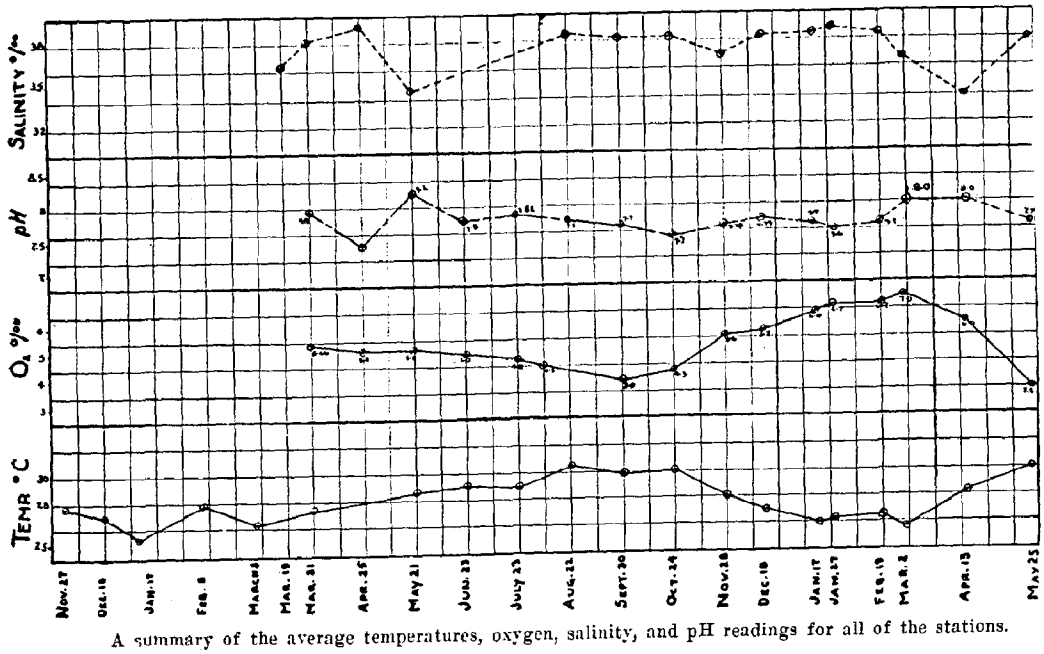
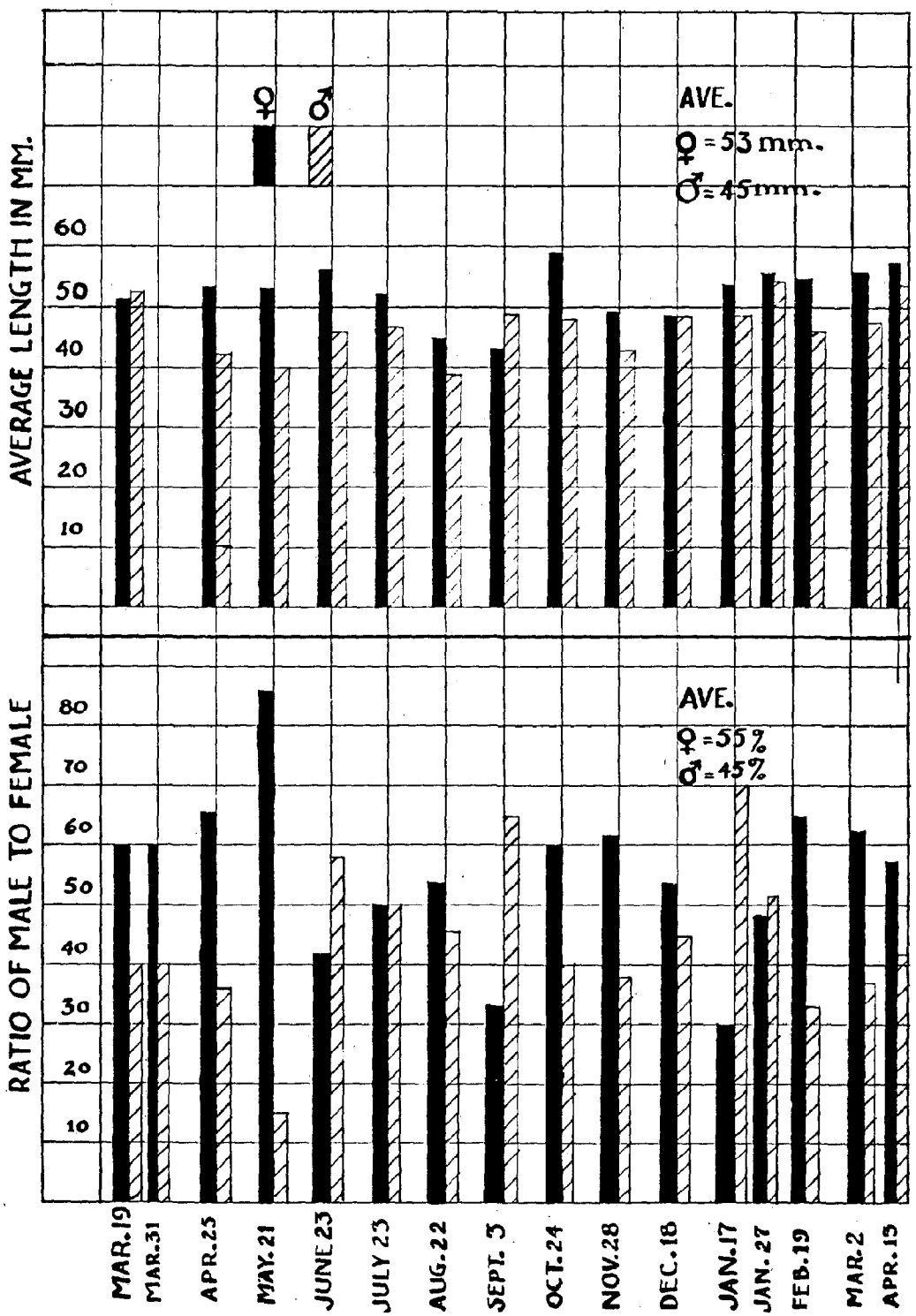


Fig. 20c. Environmental properties of lagoon with oysters in western Puerto Rico (Mattox, 1949).



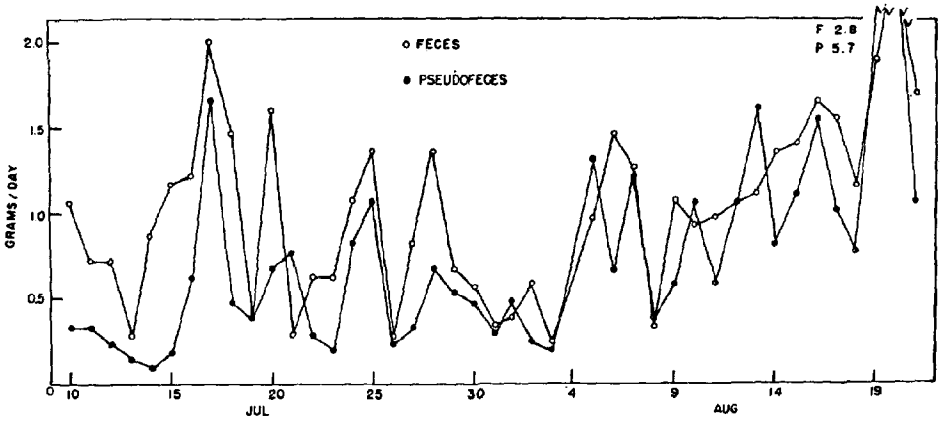
Upper graph showing average lengths of male to female shells; lower graph showing ratio of male to female animals over period from March 19, 1947 through April 13, 1948.

Fig. 20d. Even size distributions of tropical oysters in Puerto Rico (Mattox, 1949).

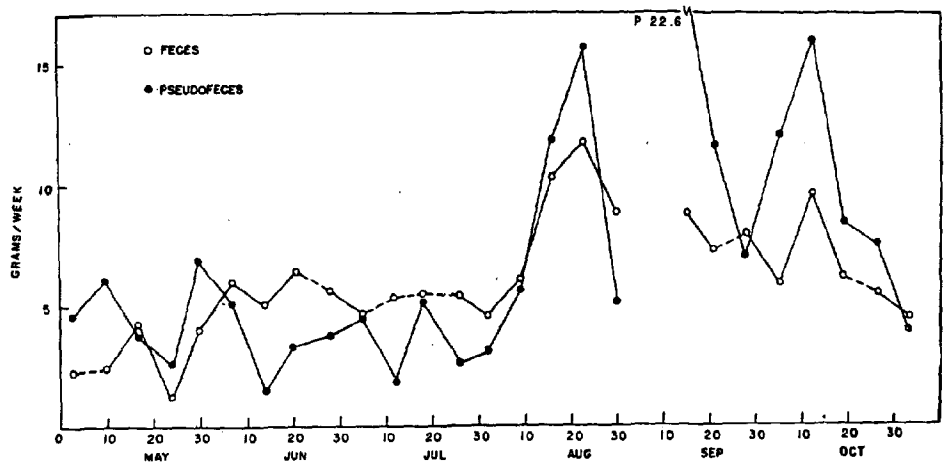
Table 4. *Biodeposition rates for several species of invertebrates*

Species	No. animals	Mean wt whole animal (g)	Mean dry wt tissue (g)	Mean deposition (g animal^{-1} week^{-1})	Mean deposition / Mean tissue weight
		14 April to 26 April 1963			
Crassostrea virginica	16	14.7	0.48	0.98*	2.0
Mya arenaria	16	18.0	1.82	0.19	0.1
Modiolus demissus	4	12.2	0.72	0.90	1.2
Balanus eburneus	53	3.4	0.09	0.03	0.3
		19 June to 14 July 1963			
Crassostrea virginica	16	36.0	1.41	1.32*	0.9
Mya arenaria	8	33.5	0.99	0.16	0.2
Molgula manhattensis	16	5.7	0.24	0.56	2.3
Balanus eburneus	39	5.4	0.08	0.02	0.2
		15 August to 29 August 1963			
Crassostrea virginica	8	30.7	1.14	1.56*	1.4
Modiolus demissus	8	19.0	0.58	0.86	1.5
Molgula manhattensis	8	2.1	0.11	0.28	2.5

* Feces and pseudofeces combined.

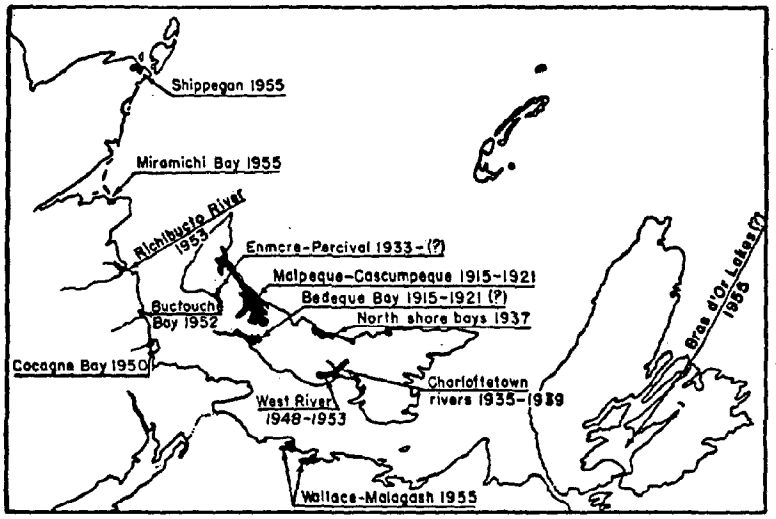


Daily rates of biodeposition for oysters, 10 July to 22 August 1962.



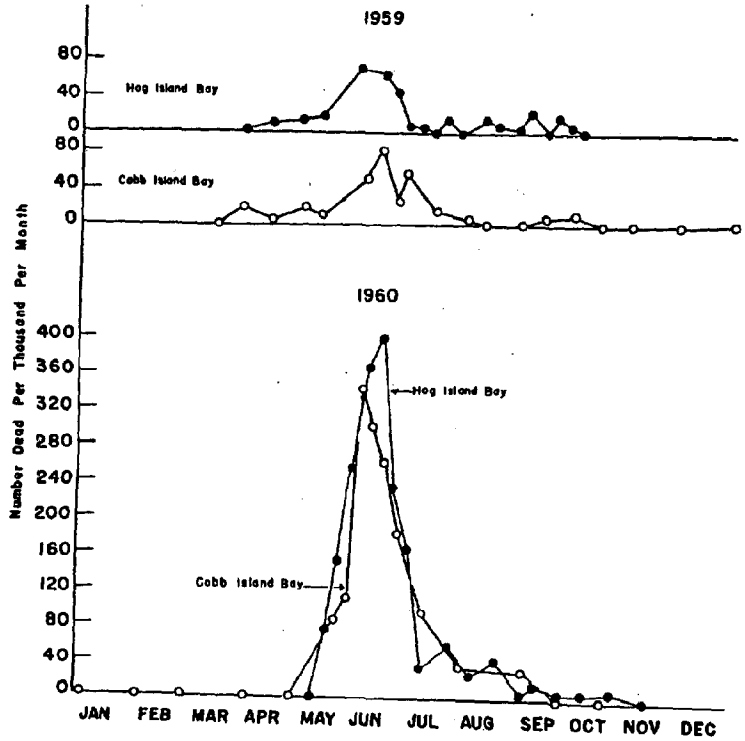
Mean weekly rates of biodeposition for groups of eight oysters, 1962. Points connected by solid lines differ statistically; those connected by dotted lines show no evidence of a statistical difference.

Fig. 21. Graphs showing feces and mucous-laden detritis (pseudofeces) released from oysters (Haven and Morales-Alamo, 1966a).



Places and times of oyster mortalities in the Maritime Provinces.

Fig. 22. Oyster locations in eastern Canada (Logie, 1956).



Death rates of native Seaside oysters in trays. Each point represents the monthly death rate for the preceding interval.

Fig. 23. Mortalities in eastern Virginia (Andrews, Wood, and Hoese, 1962).

History of Utilization

The utilization of oysters as food has led to drastic changes to natural areas with intense harvesting. Prolific natural reefs were common during colonial days along the Atlantic, Gulf and Pacific coasts. As the industry developed several stages can be noted; exploitation, depletion, restrictive legislation, management and practices of culture.

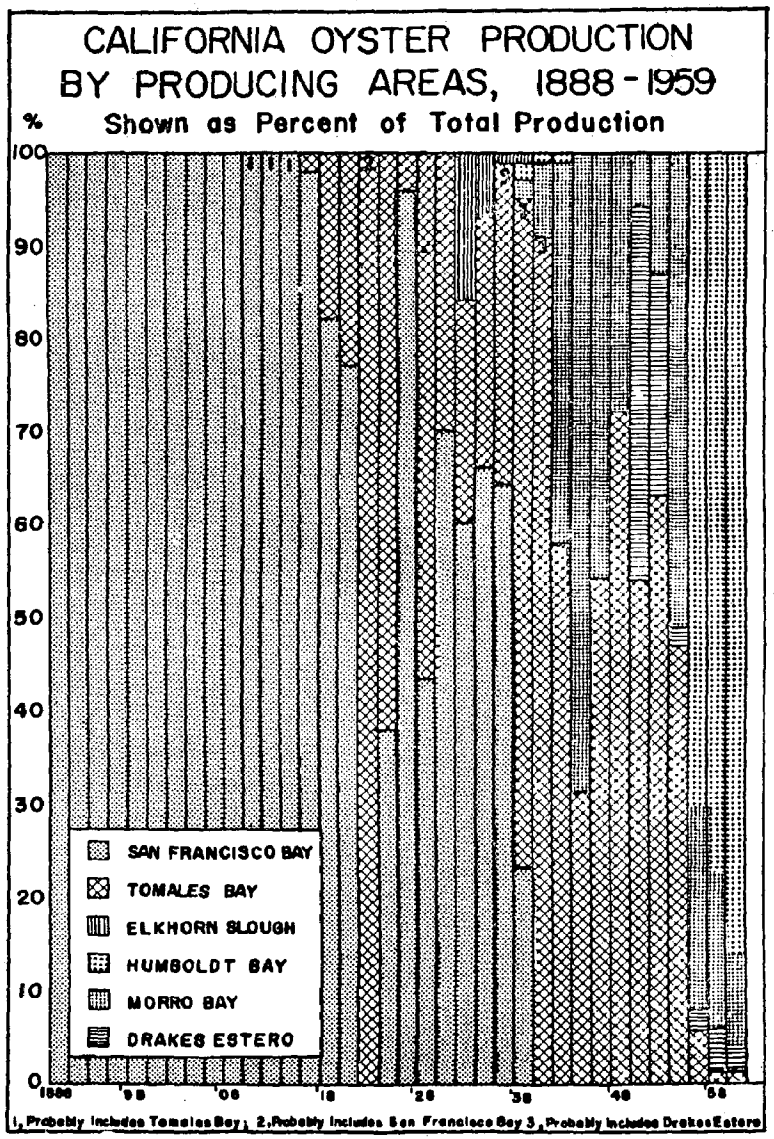
In the Long Island sound area the natural areas began to show signs of serious decline about the mid 1800's and private development had its beginning. The development of commercial packing houses in the Chesapeake Bay area resulted in a peak of harvesting near the turn of the century. Beginning about 1850 eastern oysters were shipped to California. As the demand increased large quantities of the native (Ostrea lurida) oyster were shipped from Washington to California (Barrett, E. M. 1963) (Fig. 24). Large canneries became established along the Gulf Coast and South Atlantic states utilizing oysters from natural reefs. Total production for the nation reached approximately 200 million pounds in the period from 1890-1910 and gradually declined to 54 million pounds harvested in 1965.

Through the years there has been a gradual increase in production from private based areas when compared to natural ground (See Fig. 25), (McHugh, J.L. and Bailey, R. S. 1957). Management practices adopted by states, rehabilitation programs, and importing of new species have resulted in restoration of depleted areas and development of previously barren bottom into productive areas. Importation of the Pacific oyster has resulted in an industry of approximately 10 million pounds per year since 1937 (Gunter, G. and McKee, J. 1960). The Gulf coast production has maintained fairly constant yields over the years (Fig. 26).

Many problems have confronted the oyster industry through the years: predators, diseases, closed areas because of pollution (Fig.26) and environmental factors influencing settling intensity, growth and survival. Areas previously closed for harvesting because of health hazards from domestic wastes have in cases been reopened as sewage treatment facilities have been established. Productive bottoms have been irreversibly altered by dredging and fill in many coastal states. With continued pressure from population increase and expansion of industry additional coastal areas can be expected to be altered and lost for production. This has led industry to adapt new methods such as raft culture and artificial using of oyster spat.

Disturbance

Wastes treated elsewhere in the report bear some comment in regard to oyster reefs. A broad definition of pollution is concerned with introduction of material or alteration of environment to create a detrimental situation to organisms. See, for example pulp mill waste release in Fig. 27, and some effects in Fig. 28.



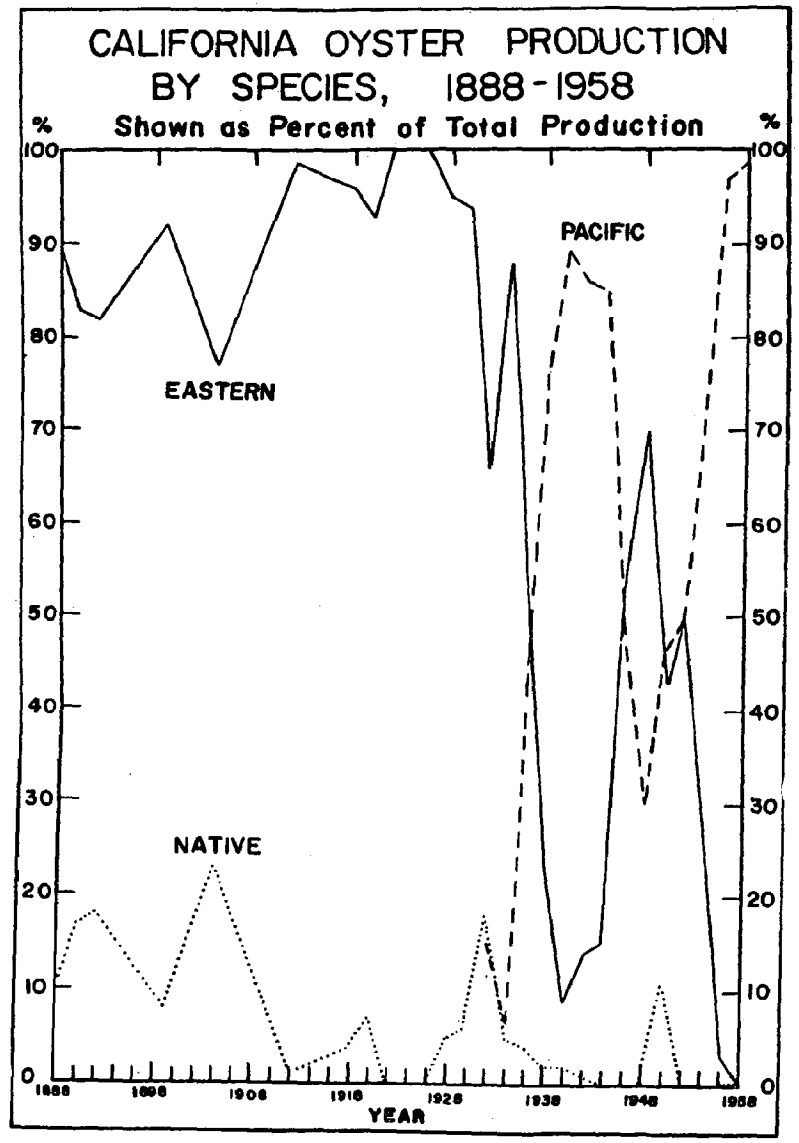
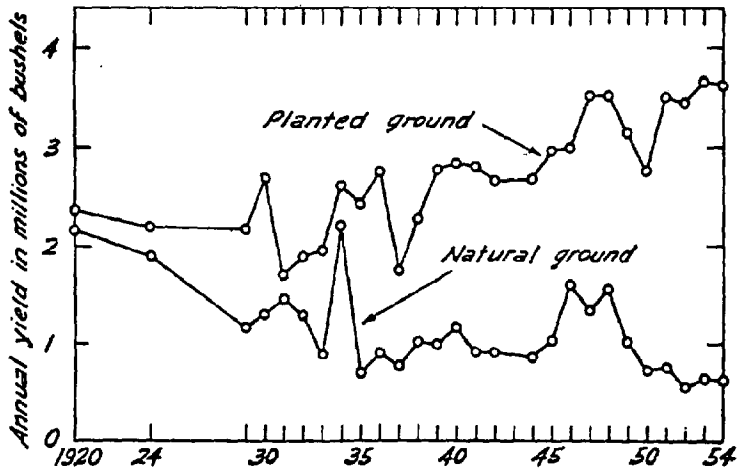


Fig. 24. Oysters in California (Barrett, 1963).



Annual landings of market-sized oysters in Virginia, 1920 to 1954.

Fig. 25. Managed and natural oysters in Virginia (McHugh and Bailey, 1957).

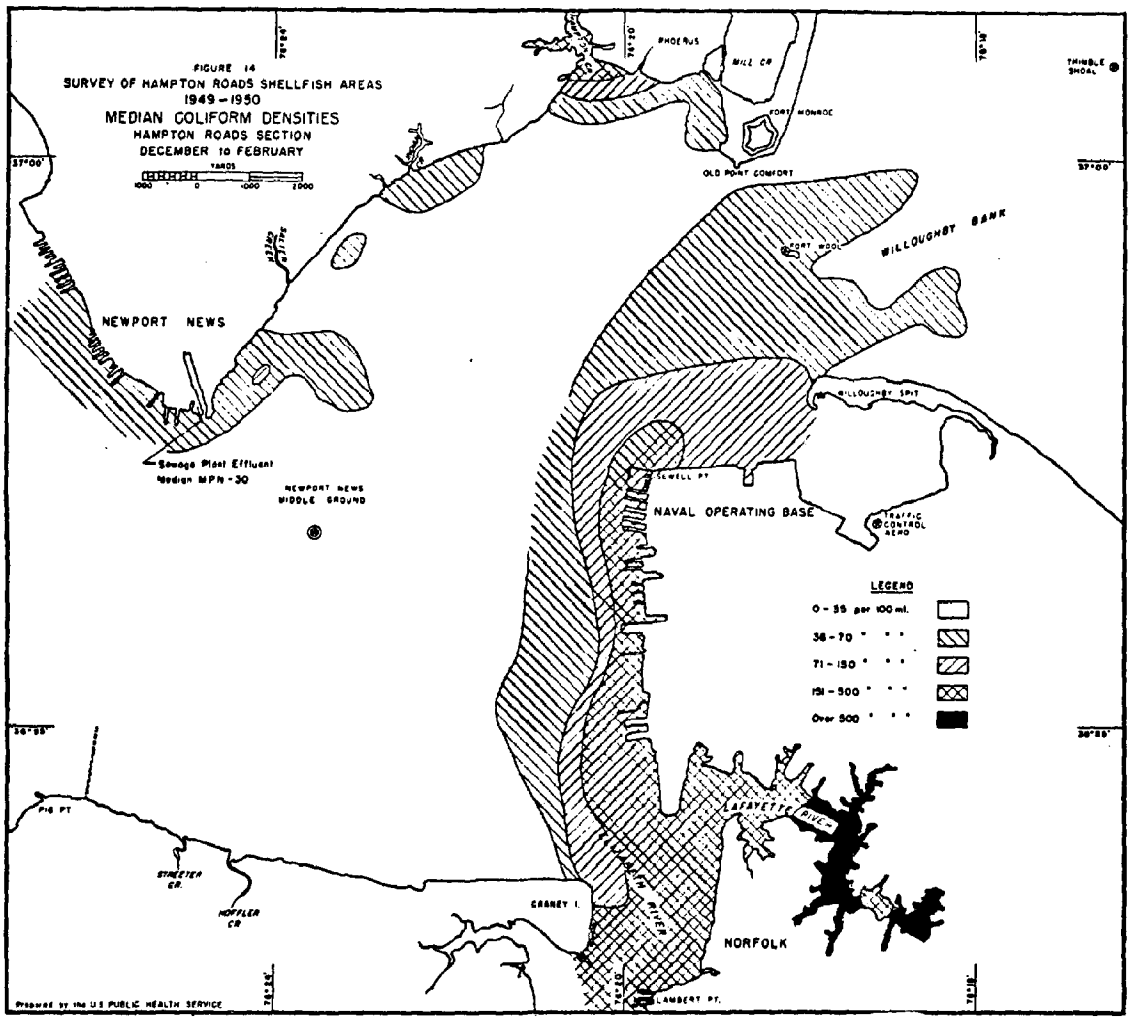
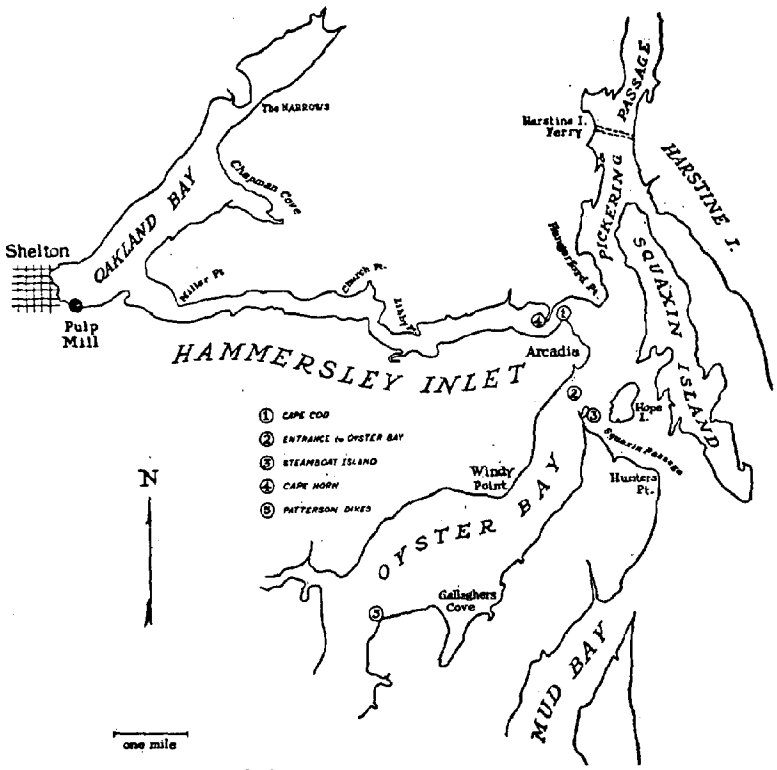


Fig. 26. Concentration of bacteria of intestinal origin in shellfish in an area receiving sewage effluents, Smith (1952).



—HAMMERSLEY INLET AND VICINITY

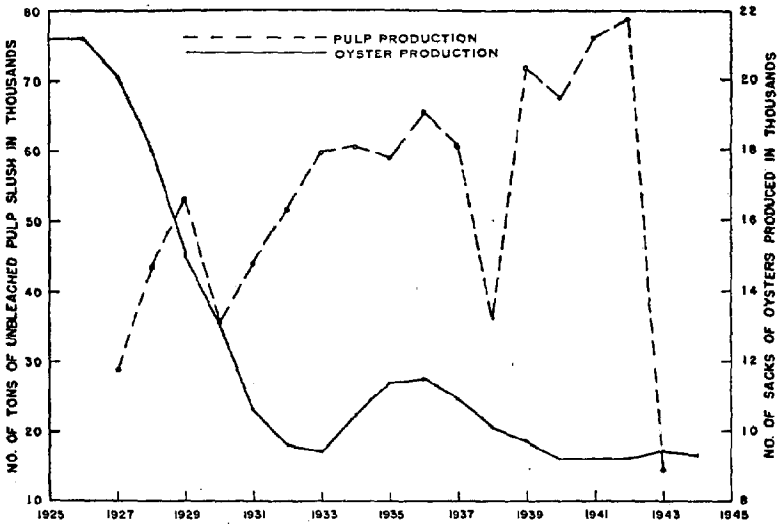
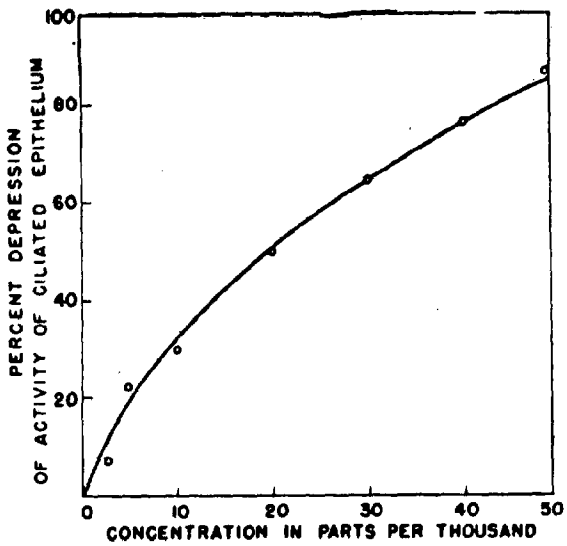
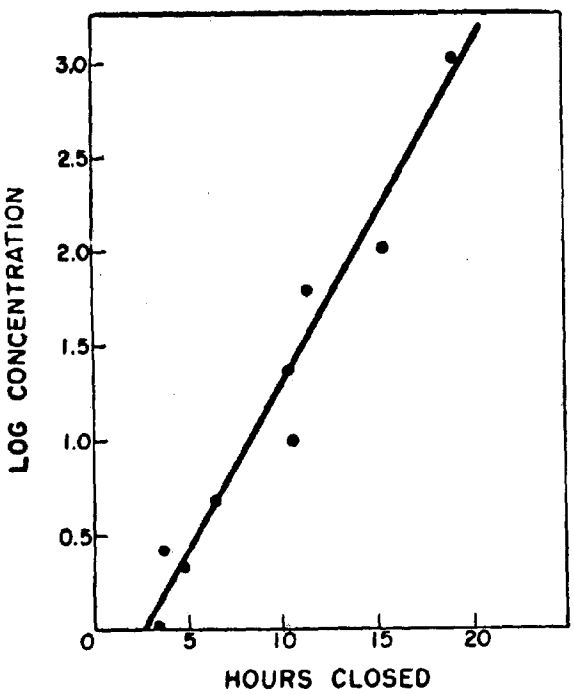


FIGURE 7—PULP MILL PRODUCTION OF THE MILL IN SHELTON, WASHINGTON, AND OYSTER PRODUCTION, 1928 TO 1945

Fig. 27. Oyster production in relation to paper pulp manufacture in Washington (McKernan, Tartar and Tollefson, 1949).

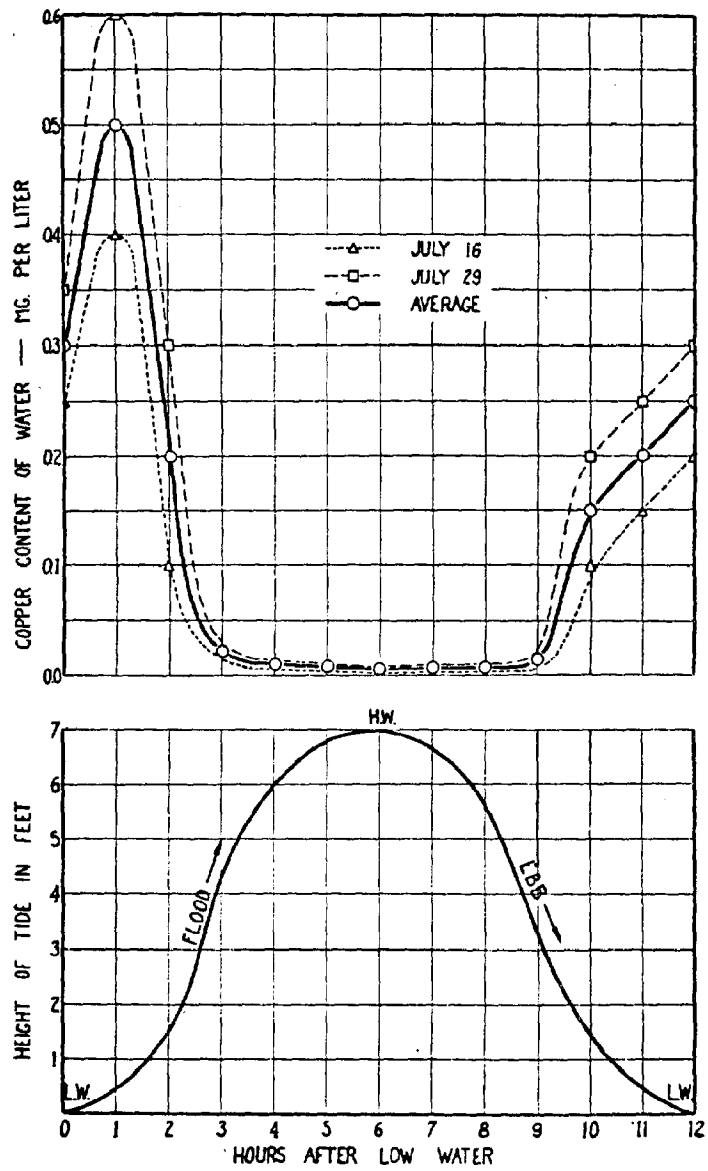


Depression of the activity of ciliated epithelium of oyster gill by increased concentration of pulp mill effluent (black liquor) of specific gravity 1.0028. From Galtsoff, Chipman, Engle, and Calderwood, 1947.



—Effect of concentration of pulp mill effluent discharged into the York River on the number of hours oysters are closed during every 24-hour period. From Galtsoff, Chipman, Engle, and Calderwood, 1947.

Fig. 28. Negative effects of pulp mill effluents on oysters.



Fluctuation in copper content during tidal cycle (low water to low water) on July 16, and July 29, 1930, Milford Harbor.

Fig. 29. Irregular exposure of oysters to harbor waters that include copper among other waste substances (Prytherch, 1934).

Depending upon the degree of alteration or amount of pollutants introduced the animals may not be affected. Domestic wastes with bacteria and virus create a health hazard to humans utilizing oysters for food but such waste at nominal levels do not influence growth and development (Fig. 27B). Usually such areas closed to commercial harvesting provide a source of seed oysters for transplanting in oyster farming and may preserve certain localities from drastic alteration from intensive harvesting. Increased volumes of domestic wastes will alter the bottom and reduce the oxygen content of waters to directly influence the population.

The increased presence in coastal waters of pesticides and related organic phosphorus and hydrocarbon components may have subtle effects through disruption of the food chain. With gradual accumulation and storage of such chemicals in tissues physiological changes may result in decreased feeding, growth rates and reproductive processes.

Oysters exposed to 1 part per billion of DDT show little obvious damage but growth rate is reduced to 20 per cent (Butler, 1966). Much residue accumulates in the ovaries. Oysters exposed to concentrations of 1 part per billion for 12 days in running sea water accumulated 25 parts per million in the eggs (Butler,1968). Apparently the animal is capable of releasing accumulated residues for oysters with 151 parts per million in tissues showed a 95 percent loss of DDT in three months after placed in unpolluted waters (Butler, 1966).

In the natural environment oysters also accumulate trace metals to levels up to many hundreds of times above the level found in the surrounding environment. With increased concentrations or constant levels present in the environment over prolonged periods, the animal may show physiological responses and eventually die. Many heavy metals considered as toxic material may be stored in the animal at levels often considered beyond a minimum lethal dosage. Some average levels of metals found in oysters show: zinc (800-1000 p.p.m.); copper (91.5 p.p.m); iron (67 p.p.m.); and cadmium (3.1 p.p.m.) (Pringle, et al, 1968). Various metals are important in the biochemical systems of the animal as enzyme activators, chelating agents and other obscure roles. Some metals are incorporated in cellular structure, or stored as compounds and later depleted in the biochemical turnover or released as cellular material. Fig. 29 is an example of trace element, copper in harbor waters that oysters concentrate.

The rate of uptake and storage of trace metals and pesticides by oysters raises the question of the ability of oysters to remove such components from the environment to a degree of stabilization. Since many of the elements are toxic and will impair the metabolic activities an optimum range of concentration probably exists beyond which the animal will suffer irreparable damage.

Chapter C-6

WORM AND CLAM FLATS

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INTRODUCTION

The bottom surfaces of estuaries develop communities of invertebrate animals (annelid worms, clams, and many other organisms) that obtain foods derived from the waters above. The flat expanses of mud and sand in the inter-tidal zone and deeper in the sub-tidal bottoms, with their associated biota, are important subdivisions of the estuary and are discussed here as sub-systems.

Estuarine flats usually have pronounced gradients in the environmental conditions, particularly with reference to salinity, temperature, tidal influence, and substrate. The tide, often a very important ecological factor, is the agent that controls the exchange of water; and its vertical amplitude determines the extent and length of time tidal flats are exposed or submerged with each tidal cycle. The strength of currents has an important influence upon the character of the sediments; in turn, the type of sediment, whether mud or sand, determines to some extent the kinds of animals that can live in the substrates. Species that inhabit an intertidal flat may also inhabit the adjacent sub-tidal substrate of the same nature. Emery and Stevenson (1957 a, b) and Hedgpeth (1957) have discussed details of the physical and chemical aspects of estuarine sediments as they apply to benthic biota.

In times of drought relatively high salinity may extend far into the estuary. Conversely, in times of freshwater flooding, the gradient zone moves nearer the inlet, leaving the bottom fauna of the inner reaches of the estuary subjected to pronounced oligohaline conditions. Permanent residents of most estuarine flats are both euryhaline and eurythermal. Survival demands that the organism be able to adjust to wider ranges of fluctuations in the environmental factors than is required in the open sea.

The number of species involved in benthic communities of estuaries is often surprisingly large. The high concentration and continuous supply of nutrients from land run-off contribute to an abundant life there, although the fauna itself is mainly recruited from the sea. While the number of species in an estuary is not as great as that in the open ocean, the number of individuals is frequently very large indeed, and this, of course, is the backbone of successful fisheries industries.

Most laymen are unaware of the abundance of animals and plants in and on the bottom surfaces of estuaries, the complexities of their interrelations, and their importance in fisheries biology. To a casual observer an exposed

sand flat or mud flat may appear largely barren, for many of the invertebrate inhabitants are burrowers and tube-dwellers, living permanently beneath the surface, while others retreat into the substrate when the tide ebbs. Most species of benthic infauna of estuaries, and about 80% of the individuals, occur in the top 15 cm. (Johnson 1967) but some of the larger species burrow to much greater depths. Relatively few species remain on the surface of an exposed flat, yet a group of biology students, equipped with shovels and rakes, can in a half hour collect between 60 and 80 species of macro-fauna from such a flat in a temperate region estuary. This does not include the numerous species of microorganisms and meiofauna that could be obtained by sifting the substrate. Neither does it include the birds that feed on the flat, nor the fishes and crabs that move in when the tide rises and water again covers the flat.

Even many fisheries biologists, intent on the study of a single commercial species in isolation from its biological environment, are unaware of the vast numbers of organisms involved in the ecosystem of a sand flat or mud flat. In Long Island Sound, Sanders (1956) found that the mean number of benthic animals varied from 5,563 to 46,398 per square meter. Sanders, Goudsmit, Mills and Hampson (1962), in an intensive investigation of several localities on the intertidal flats of Barnstable Harbor, Massachusetts, found the number of benthic animals to range from 7,000 to 355,000 per square meter. Most of these organisms are small in size, but together they play a far more important part in the biological economy of the flats than do the larger but less numerous individuals of commercial importance. In some communities the majority of individuals (70% or more) are concentrated in relatively few species.

EXAMPLES

Flats With High Exchange Rates; Barnstable Harbor, Mass.

Barnstable Harbor on the north shore of Massachusetts is a much studied bay in which sandy flats are located between the marsh and the open sea (Figs. 1 and 2). The tidal range is large relative to the depth (Table 1) so that larvae released from bottom invertebrates tend to be washed out of the bay. Ayers (1956) has calculated flushing rates necessary for stable populations of clams as a function of larval survival. As shown in Fig. 2 there are also sharp changes in salinity with tidal cycles which restrict the number of species that can exist in the bay. The detailed and extensive two year study by Sanders, Goudsmit, Mills, and Hampson (1962) of the large intertidal flats presents an excellent example of the abundance of fauna in the substrate and the feeding relations among the different types of organisms (See Table 2). Other investigators working on the same flats have added supplementary data (Ayers 1956, 1959; Mangum 1964; Moul and Mason 1957). What is now known about these flats applies generally to many others.

Sanders et al reported 82 species of substrate invertebrate animals, with numbers of individuals at six different stations ranging from $7000/m^2$ to $355,000/m^2$. For the pea clam (*Gemma gemma*) they recorded an average

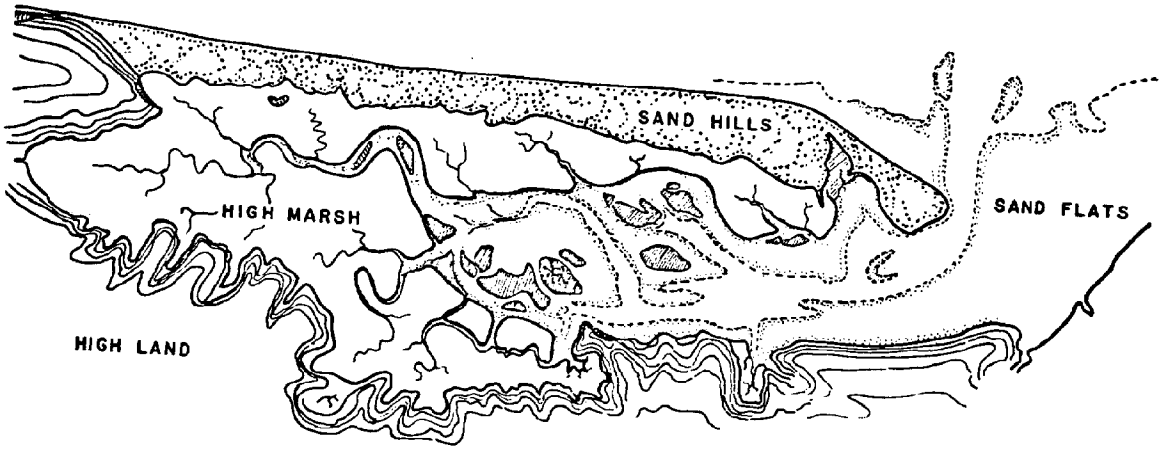


Fig. 1. Map of the Barnstable area (From Redfield 1959).

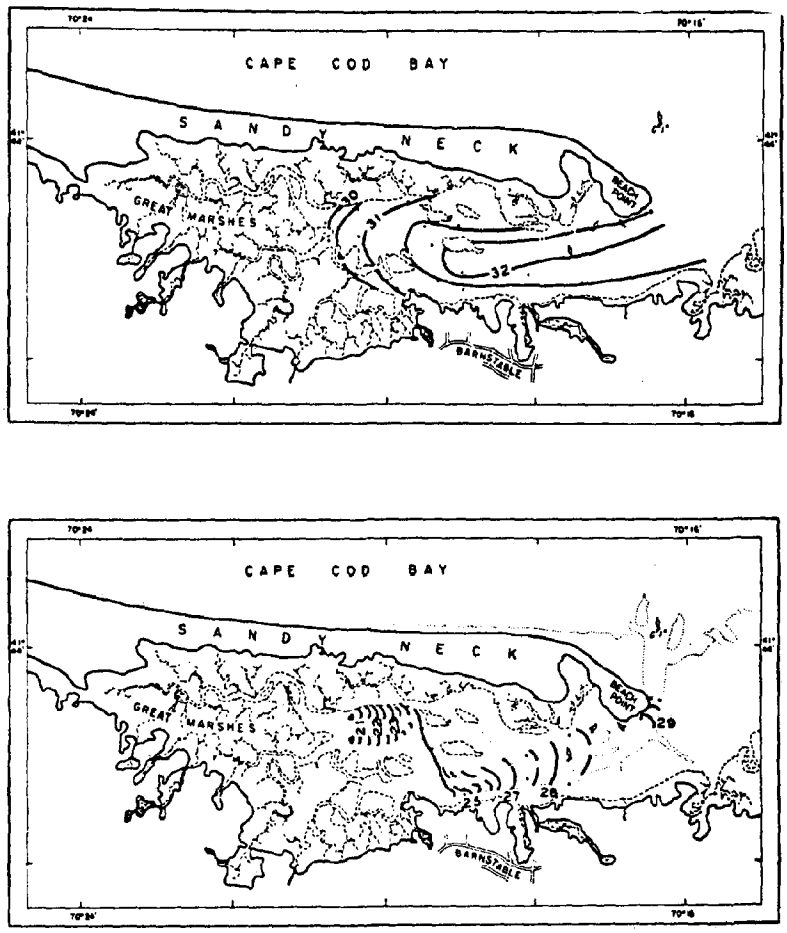


Fig. 2. Distribution of surface salinity (0/00) at Barnstable Harbor during spring freshet, April 12 and 16, 1948. Above: at high water. Below: at low water. (From Ayers 1959; Fig 5)

Table 1. Tidal current velocities at surface and bottom during the first half of a flooding tide over the sand flat at Station A, Barnstable Harbor on July 29, 1959. (From Sanders, Goudsmit, Mills, and Hampson 1962; Table 1)

Time	Depth (cm)	Velocity (cm/sec)		Bottom vel/Surface vel
		Surface	Bottom	
1530	14	9.8	8.1	0.83
1545	24	13.3	8.7	0.65
1600	34	22.2	12.9	0.58
1615	45	23.8	14.3	0.60
1630	56	27.0	16.4	0.61
1645	70	31.3	18.2	0.58

Table 2. Some benthic invertebrates of Barnstable Harbor, Massachusetts with stomach content data (From Sanders, Goudsmit, Mills, and Hampson 1962; Table 4).

Species	No. of individuals
NEMERTINEA:	
Amphiporus sp.	(2) sand, benthic diatoms
	(7) empty
Cerebratulus lacteus	(1) setae of polychaete, Gemma shells, Hydrobia, Odostomia, young Mytilus, filamentous algae, diatoms, detritus, sand
	(1) 5 Hydrobia, many polychaete setae, ostracod, sand
Micrura leidyi	(1) polychaete setae, sand
	(3) empty
POLYCHAETA:	
Eteone heteropoda	(1) few diatoms, detritus, sand
	(1) few diatoms, strands of filamentous algae, sand
	(1) diatoms, sand
	(1) detritus, sand
	(2) empty
Nereis caudata	(1) sand, detritus
	(2) sand, detritus, diatoms
	(4) sand, diatoms
Nereis virens	(1) sand, diatoms, detritus, small Gemma, filamentous algae
Glycera dibranchiata	(1) sand, many bundles of polychaete setae
	(1) sand
	(17) empty
Lumbrinereis tenuis	(1) sand, diatoms
	(2) sand, diatoms, detritus
	(1) empty
Drilonereis longa	(1) sand, diatoms, filamentous algae
	(1) empty
Diopatra cuprea	(1) sand, Gemma, Hydrobia, much filamentous algae (Ulva), detritus, crustacean setae, and spines
	(1) sand, Gemma, 2 Hydrobia, much filamentous algae (Ulva), detritus
	(1) sand, filamentous and thallos algae, 2 Gemma, 4 Hydrobia
	(1) sand, thallose algae, diatoms, Gemma
	(2) sand, thallose algae, diatoms
Streblospio benedicti	(5) sand, detritus
	(4) sand, diatoms
	(3) sand, diatoms, detritus
	(1) detritus, diatoms
	(2) empty
Pygospio elegans	(2) sand, diatoms
	(8) sand
	(8) empty
Nerinides agilis	(2) sand, diatoms
	(2) sand
	(13) empty
Polydora ligni	(2) sand, diatoms
Spio setosa	(1) sand, many diatoms, filamentous algae, detritus, nematode
	(1) sand, detritus, unidentified disc-like objects
Heteromastus filiformis	(2) sand, detritus
	(2) sand, detritus, diatoms
	(1) sand, diatoms
	(5) sand
Tharyx sp.	(2) sand, diatoms
	(2) sand
	(3) empty
Scolopos robustus	(1) sand, diatoms
	(1) detritus, diatoms
Scolopos fragilis	(2) sand, diatoms, detritus
	(2) sand, diatoms, detritus, macroalgae, possible animal material
Clymenella torquata	(3) sand, detritus, diatoms
	(3) sand, detritus
	(3) sand, detritus, disc-like objects
	(2) sand
	(9) empty
Amphitrite ornata	(1) sand, detritus, diatoms, Gemma, Eteone
	(2) sand, detritus, diatoms, Gemma
	(1) sand, detritus, diatoms

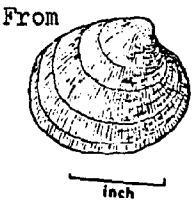
Table 2 continued

Species	No. of individuals
ECHINODERMATA:	
Leptosynapta inhaerens	(1) sand, detritus, diatoms
	(2) sand, detritus
	(1) sand, detritus, diatoms, 1 Gemma
	(1) sand, detritus, 3 Gemma, 1 ostracod
	(1) sand, detritus, 3 young Gemma, 1 adult Gemma, 2 Hydrobia, crustacean appendage, broken shells, diatoms, disc-like objects
ENTEROPNEUSTA	
Saccoglossus kowalevskii	(2) sand, detritus, diatoms
	(1) sand
	(4) empty
MOLLUSCA:	
Gemma gemma	(17) empty
Mya arenaria	(2) empty
Ensis directus	(1) empty
Tellina agilis	(1) sand, diatoms, detritus
	(1) sand, diatoms
	(1) diatoms
Aligena elevata	(6) sand, diatoms, unicellular algae
	(1) sand, diatoms
	(1) sand
	(2) empty
Hydrobia minuta	(1) diatoms
	(1) empty
Retusa pertenius	(4) sand
	(1) empty
Polynices duplicata	(1) empty
CRUSTACEA:	
Edotea montosa	(1) diatoms, filamentous, and thallose algae, ostracod
	(1) few polychaete seta
	(4) empty
Listriella clymenellae	(4) empty
Carinogammarus mucronotus	(1) sand, diatoms, detritus, macroalgae
	(1) sand, diatoms, detritus
	(1) empty
Crago septemspinosus	(1) sand, detritus, diatoms
	(1) sand, detritus, ostracods, small crustacean limb
	(1) sand, diatoms, ostracods, nematodes, many crustacean limbs, mollusc shells (?Gemma)
	(1) sand, Gemma shells, many diatoms, much green algae, nematodes, small crustacean fragments
	(1) sand, broken shells, 2 Gemma, detritus, nematodes, diatoms, much thallose algae
Eupagurus longicarpus	(1) sand, much filamentous algae of various spp., few diatoms

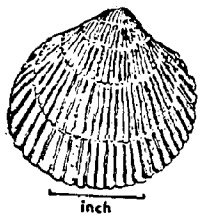
Table 3. West coast bay clams and their relative abundance (From Marriage 1958, Table 2; Kirk 1967).

River or Bay	Gaper	Cockle	Softshell	Butter Clam	Littleneck
Nehalem	0	0	2	0	0
Tillamook	3	3	2	1	1
Netarts	3	3	1	2	1
Nestucca	0	0	1	0	0
Salmon	0	0	1	0	0
Siletz	0	0	1	0	0
Yaquina	3	3	2	1	1
Alsea	1	1	2	0	0
Siuslaw	1	0	2	0	0
Umpqua	1	0	3	0	0
Coos Bay	3	2	1	1	1
Coquille	0	0	1	0	0

0—not known to be present
1—present but scarce
2—fairly abundant
3—present in considerable abundance



BUTTER CLAM
Saxidomus giganteous



COCKLE
Cardium corbis

density of 146,000 per square meter and a maximum density of 331,000 (Fig. 3a). The large numbers can be accounted for by the fact that this is a benthic invertebrate without planktonic larval stages, and the young remain in the vicinity of the adults. Occurring in such great abundance, Gemma gemma must be an important species in the ecology of the flat. The soft shell clam Mya arenaria also occurs in some years, after good larval release and set have established a population (Fig 3b).

Surf Clam Beds

In northern climates where wave energies are large on exposed sandy bottoms simple benthic communities may develop, dominated by deep digging surf clams. Examples of their distribution in Massachusetts are given in Fig. 4. On the west coast the surf clam is a razor clam, Siliqua patula (Fig.5 a). Fig.5b presents monthly shell length data for S. patula in Oregon, indicating that the main growth occurs in the spring.

Fluctuating, Low Salinity Clam Beds

In the upper zone of temperate river estuaries where salinities fluctuate with tide, runoff, and season clam flats tend to be dominated by the soft shell clam Mya arenaria which buries itself far below the surface (Fig.3b). In bottoms scoured by waves and flood, and subjected to extreme winter cold and to predators that eat the unshielded siphons, the deep location is adaptive. The occurrence of Mya in the shoreward, shallower, and more severe zones of a northern estuary (North River, Mass.) is illustrated in Fig. 6.

On the West Coast, Mya beds are found in the upper reaches of Oregon estuaries. Maps of Yaquina Bay, for example (Figs. 7 and 8), show Mya in the lowest salinity range.

In warmer locations with reduced tides other clam species, especially Rangia, replace Mya (See Oligohaline Chapter).

High Salinity Flats

At high salinity and more stable conditions of temperature and depth, diversity of species increases along with specialization. Examples of high salinity flats on the east coast are those of the Cape Cod region of Massachusetts predominated by the quahog clam, Mercenaria. Fig. 9 shows quahog distribution in small bays and salt ponds of the area. Growth of the quahog is illustrated in Fig. 10. Distribution of this and other species in Greenwich Bay, Rhode Island, is given in Fig. 11. Worm components of the high salinity flats of Rand's Harbor, Massachusetts are shown in Figs. 12 and 13. On the west coast the clam niches are divided among several species as indicated in Table 3. West coast examples are the lower reaches of the Yaquina estuary (Figs. 7 and 8) and Tomales Bay, California (Fig. 14).

A variety of kinds of bottom communities are found in the environs of Beaufort, N. C. (Fig. 15; Table 4). Diagrams of some of the principal worms found

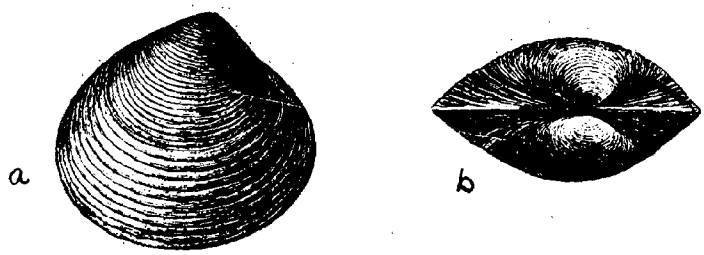


Fig. 3a. The pea clam, Gemma gemma (From Abbott 1955; Fig. 84).

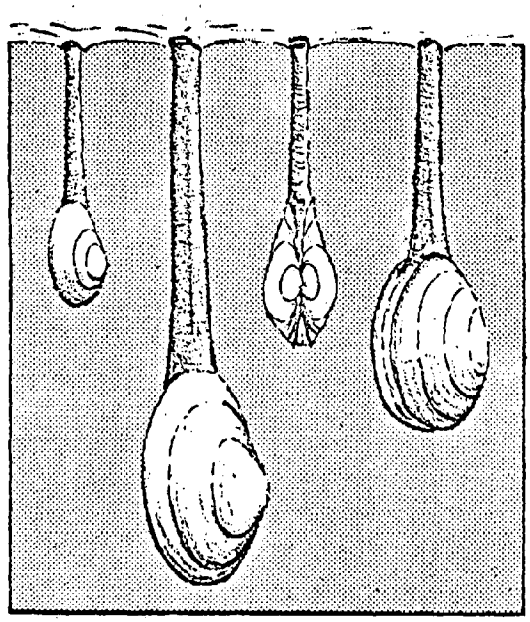


Fig. 3b. The soft-shelled clam, Mya arenaria (From Pfitzenmeyer and Shuster 1960).

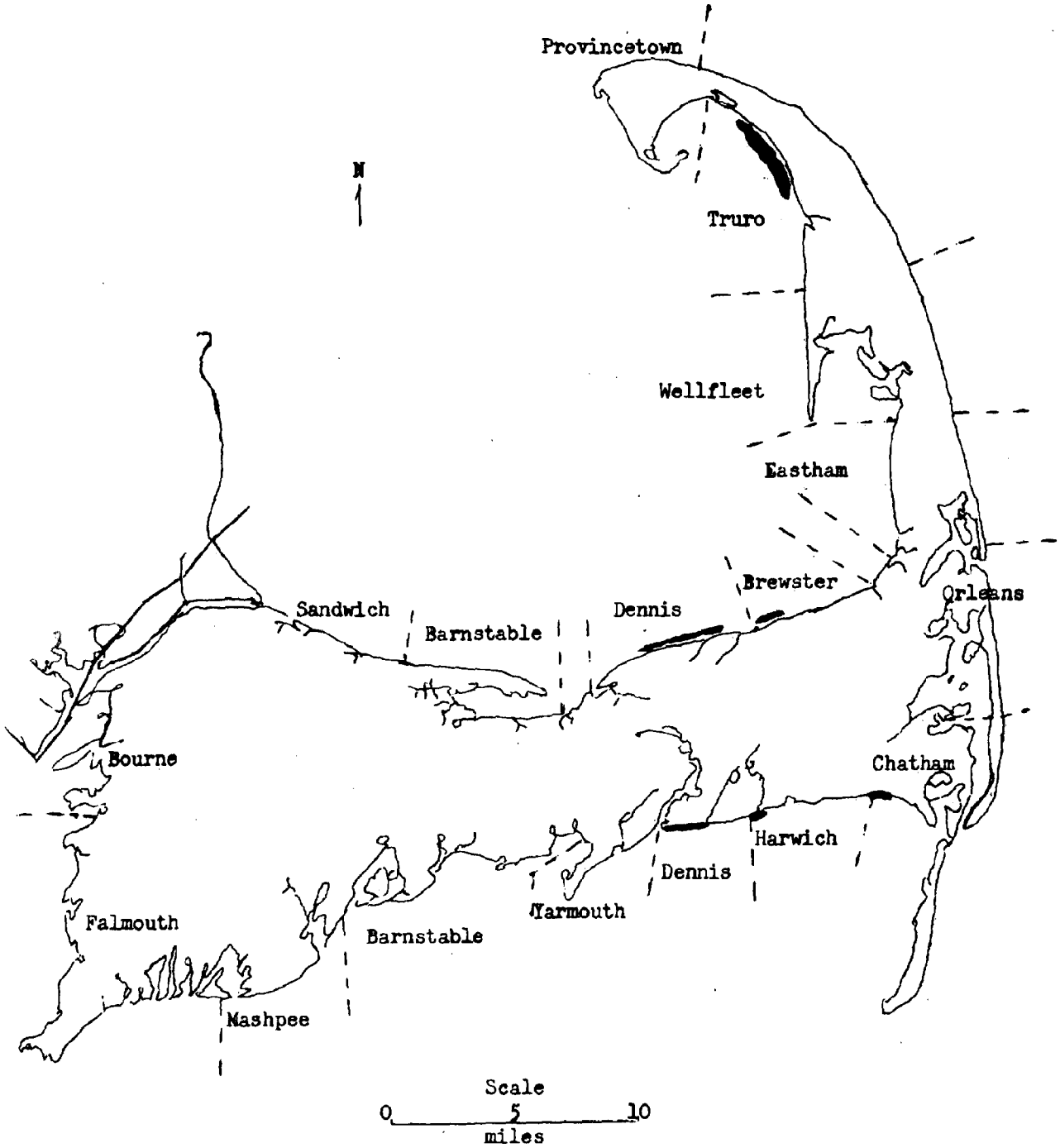


Fig. 4. Distribution of surf clams in Barnstable County, Mass. in 1964 (From Massachusetts Division of Marine Fisheries. Annual Report for 1964).

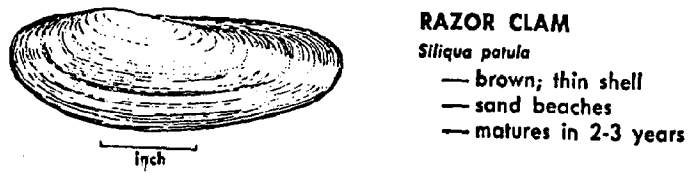


Fig. 5a. Siliqua patula, the west coast surf clam (From Kirk 1967).

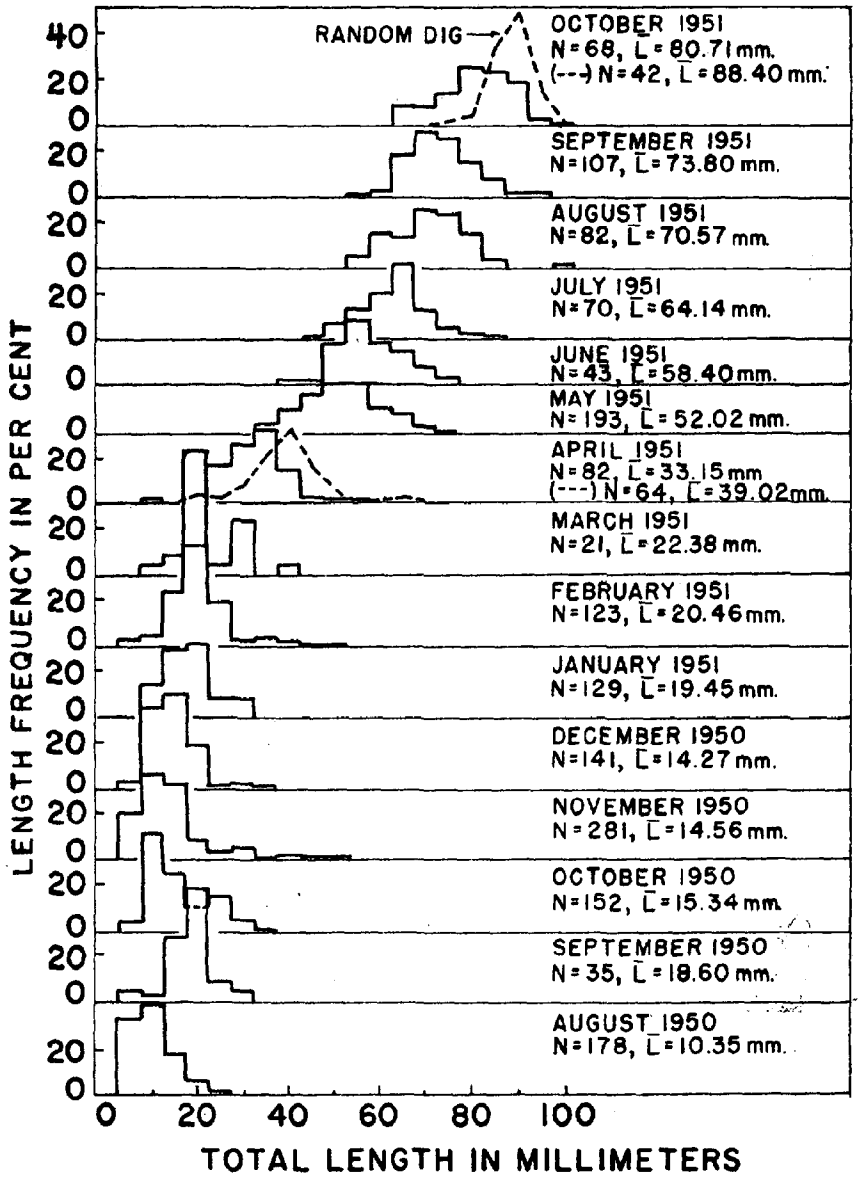


FIGURE 11. GROWTH OF THE 1950 YEAR CLASS, AUGUST 1950—OCTOBER 1951, FROM CLAM SAMPLES ORIGINATING 1.3 MILES NORTH OF THE *PETER IREDALE*.

Fig 5b. Growth rates of Siliqua patula in Oregon (From G. Hirschhorn 1962).

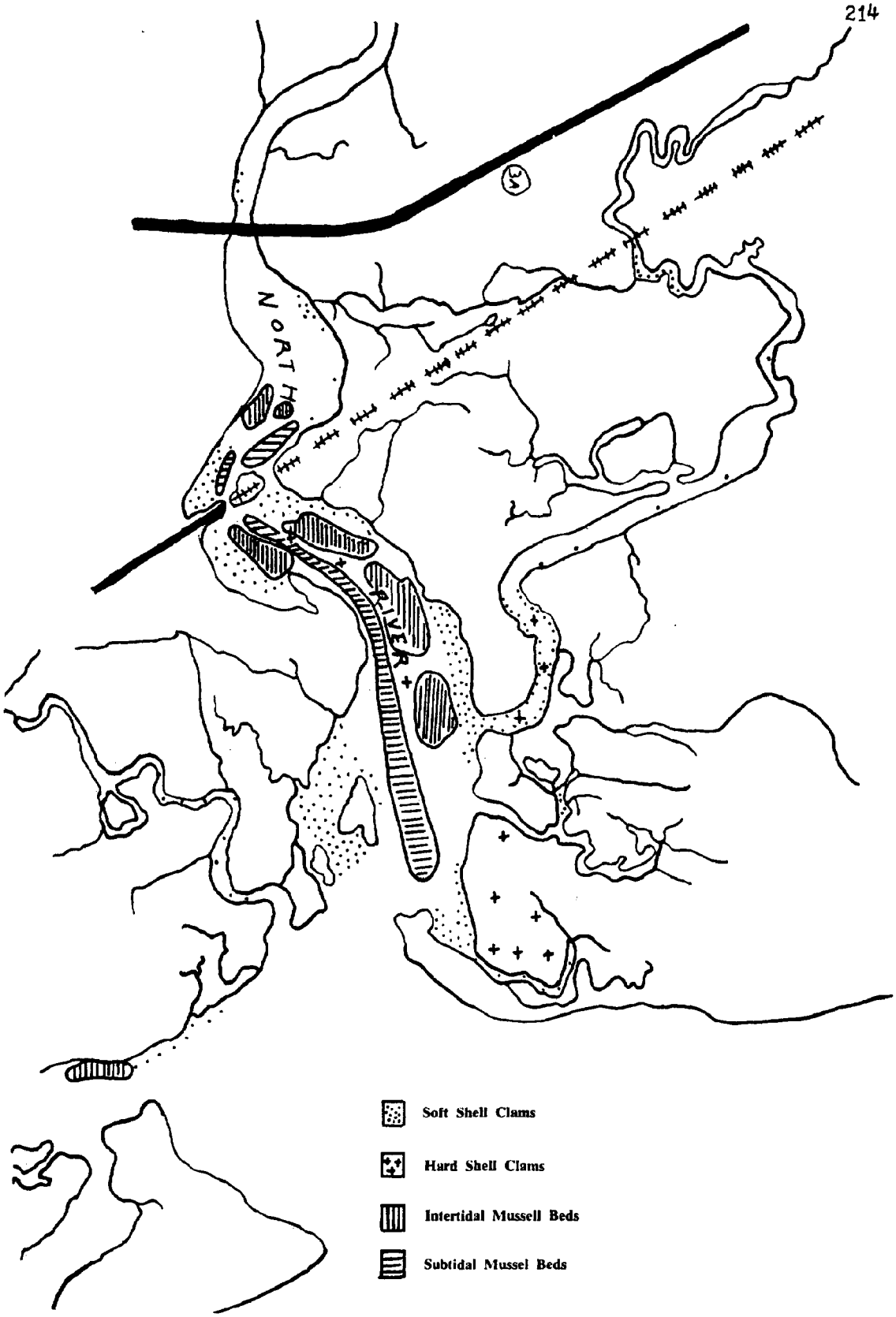


Fig. 6. Distribution of soft shell (Mya arenaria) and hard shell (Mercenaria mercenaria) clams and mussels (Mytilus edulus) of the North River, Massachusetts (From Fiske, Watson, and Coates 1966; Fig. 8).

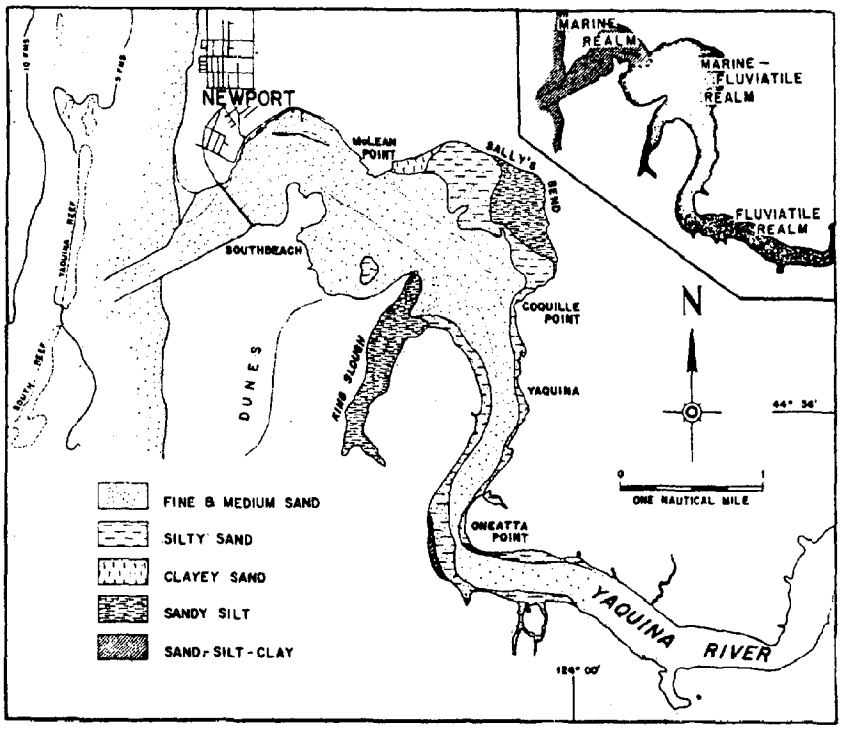


Fig. 7. Deposition and sediment types in Yaquina River estuary, Oregon, according to the nomenclature of Shepard, 1954 (From Kulm and Byrne 1966; Fig. 7).

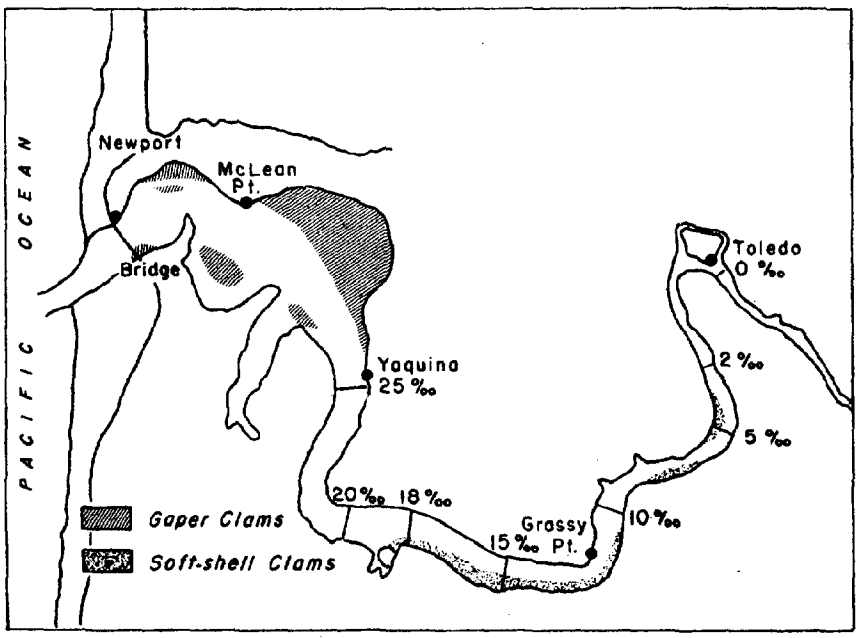


Fig. 8. Distribution of gaper and soft shell clams in the Yaquina River estuary (From Burt and McAlister 1959; Fig. 7).

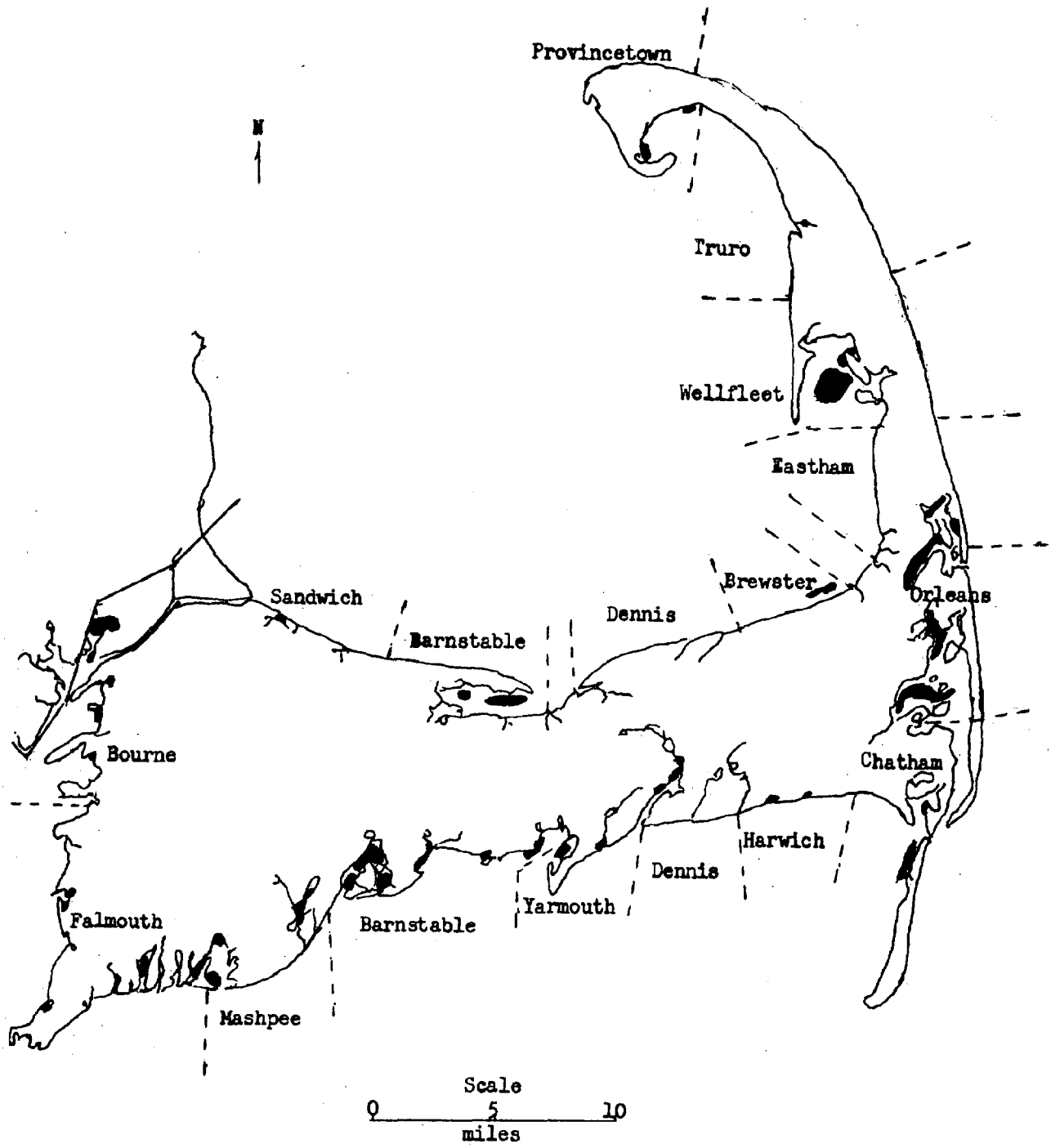


Fig. 9. Distribution of the quahog clam, Mercenaria, in Barnstable County, Mass. in 1964 (From Massachusetts Division of Marine Fisheries. Annual Report for 1964).

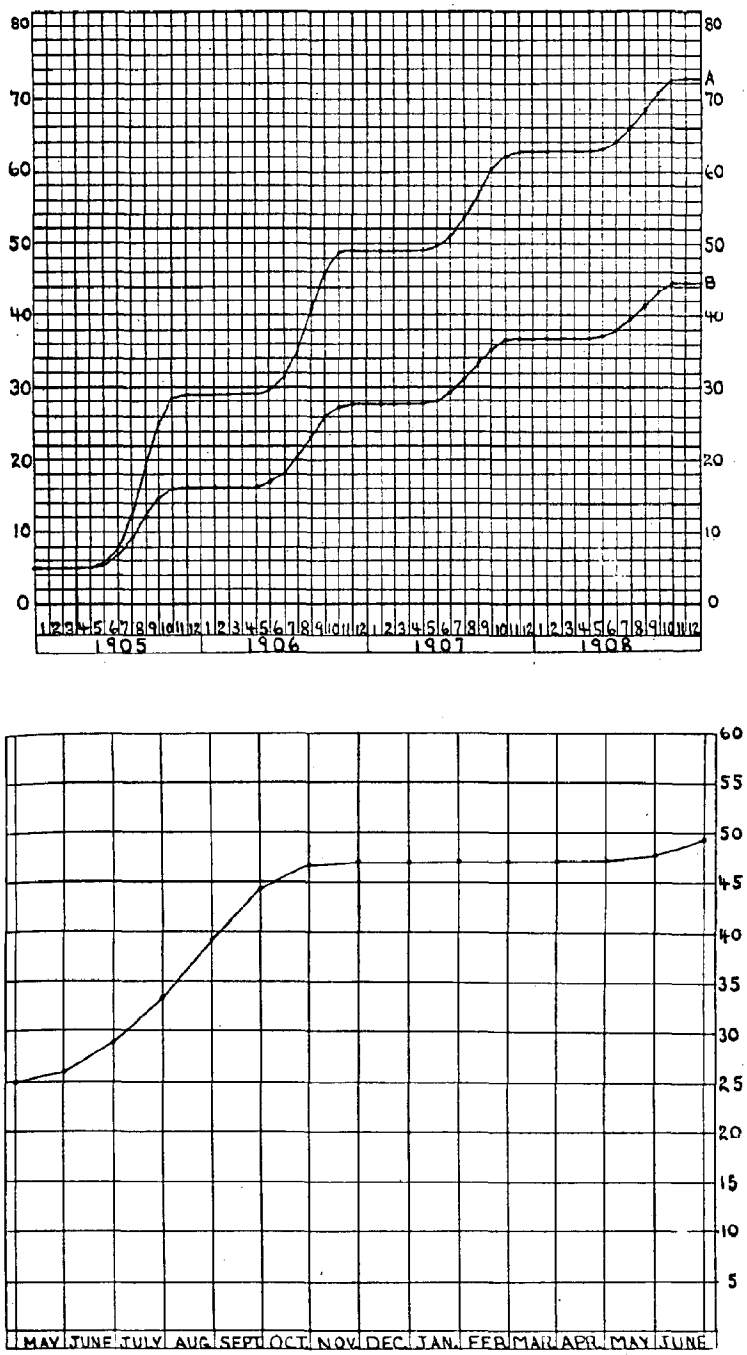
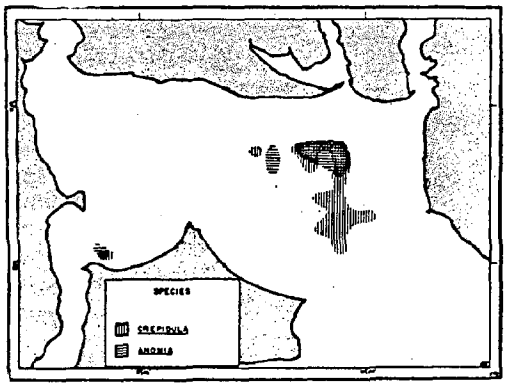
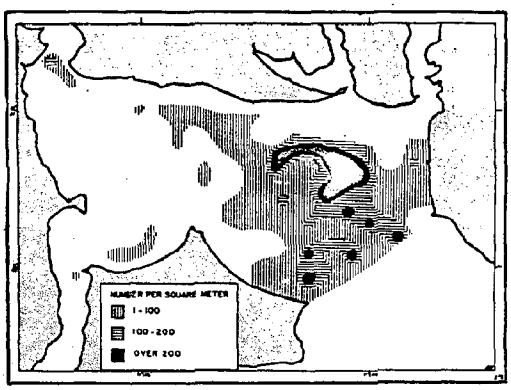


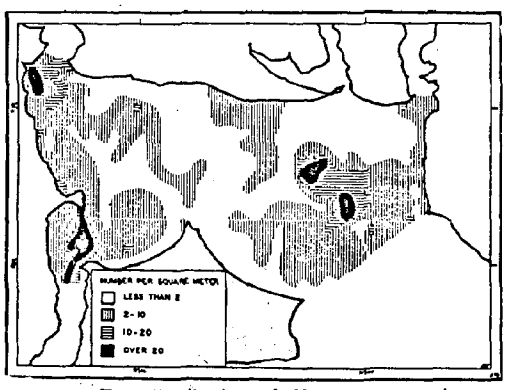
Fig. 10. Growth records of the quahog clam, Mercenaria mercenaria (From Belding, 1912).



The distribution of *Crepidula fornicata* and *Anomia simplex* in 1951.

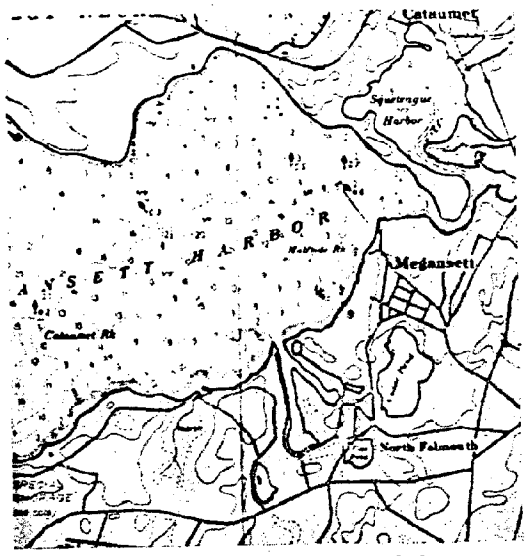


The distribution of *Nereis succinea* in 1952.

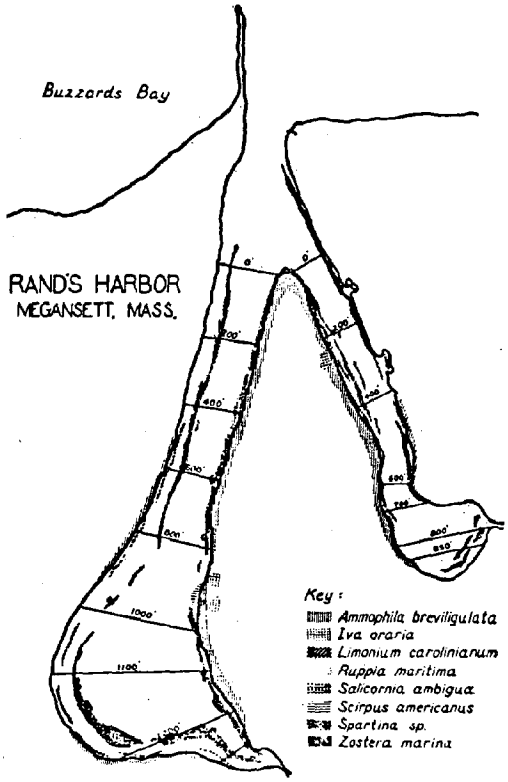


The distribution of *Venus mercenaria* over 15 mm. in length in 1957

Fig. 11. Distribution of several species of bay fauna in Greenwich Bay, Rhode Island (From Stickney and Stringer 1957, Figs. 5, 6, and 7).

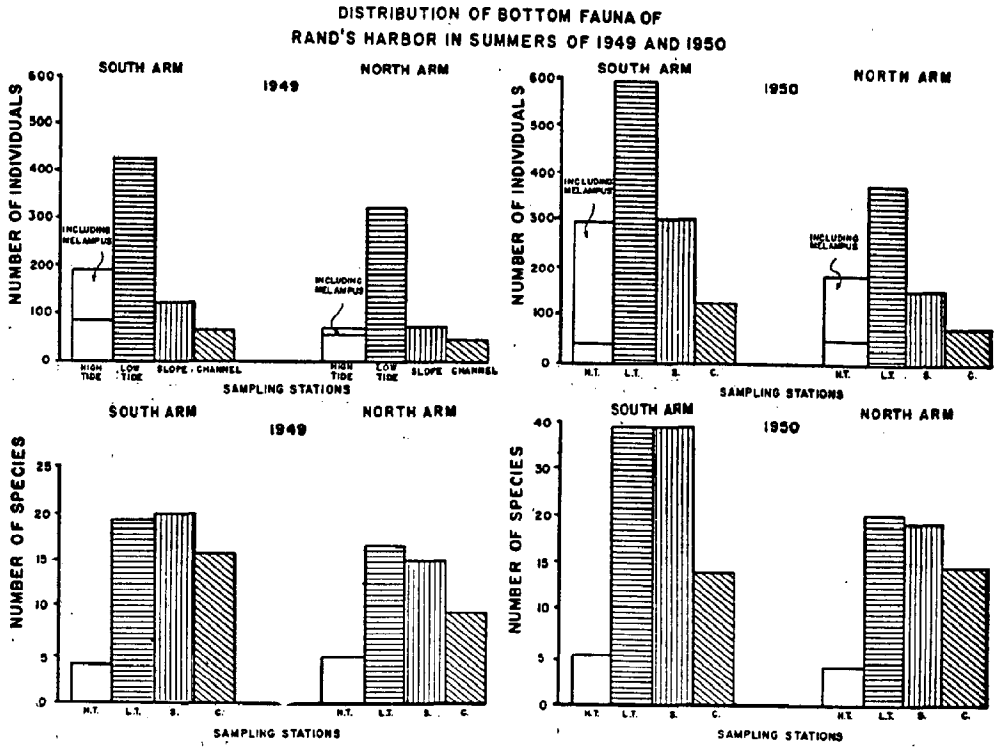


Map of area studied. Rand's Harbor appears as a Y-shaped body of water opening into Megansett Harbor, an arm of Buzzards Bay. (North is toward the top of the map.) Scale: 1 in. equals 2080 ft.

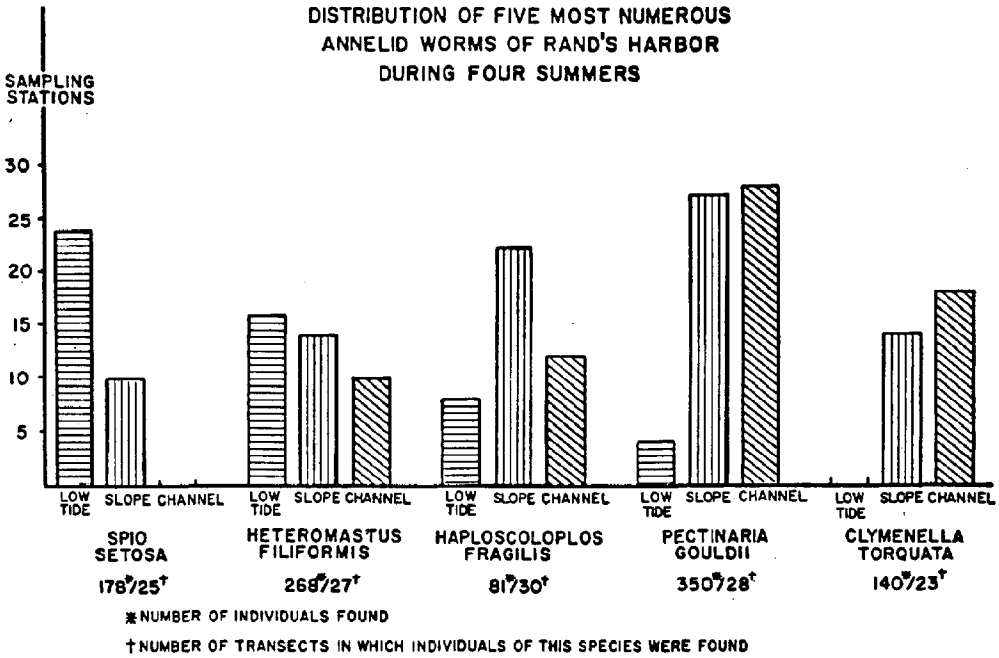


Map of Rand's Harbor showing the location of rooted vegetation.

Fig 12. Maps of Rand's Harbor, Massachusetts (From Burbanck, Pierce, and Whiteley 1956, Figs. 1 and 3).



Numbers of individuals and species of invertebrate animals living in Rand's Harbor at high tide and low tide levels and channel during the summers of 1949 and 1950.



Distribution of the five most numerous species of annelid worms in Rand's Harbor during the summers of 1946, 1948, 1949, and 1950. Asterisk indicates total number of individuals of each species taken during four summers. Dagger indicates the total number of transects from which species were taken.

Fig. 13. Distributions of invertebrates living in Rand's Harbor, Mass. (From Burbanck, Pierce, and Whitely 1956, Figs. 11 and 12).

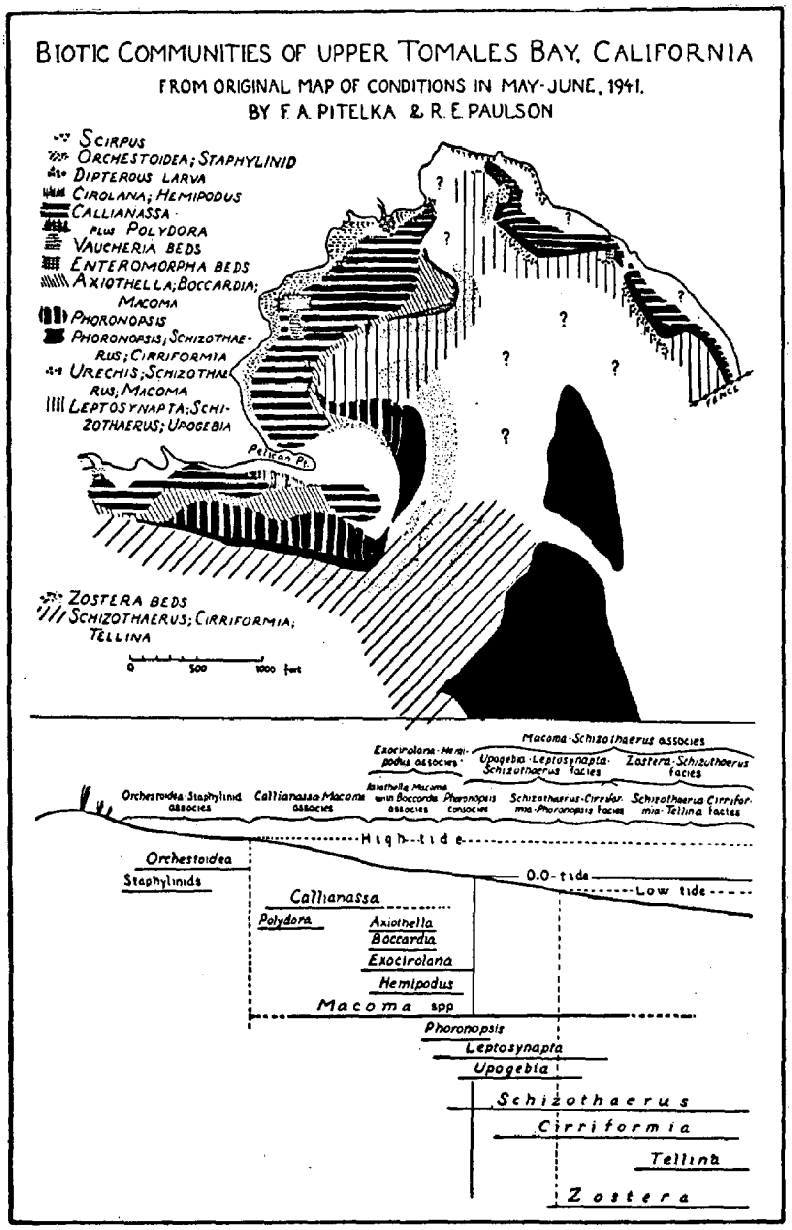


Fig. 14. Map of upper Tomales Bay, California showing biotic communities and their zonation according to tides (From Emery 1960 , after Pitelka and Paulson).

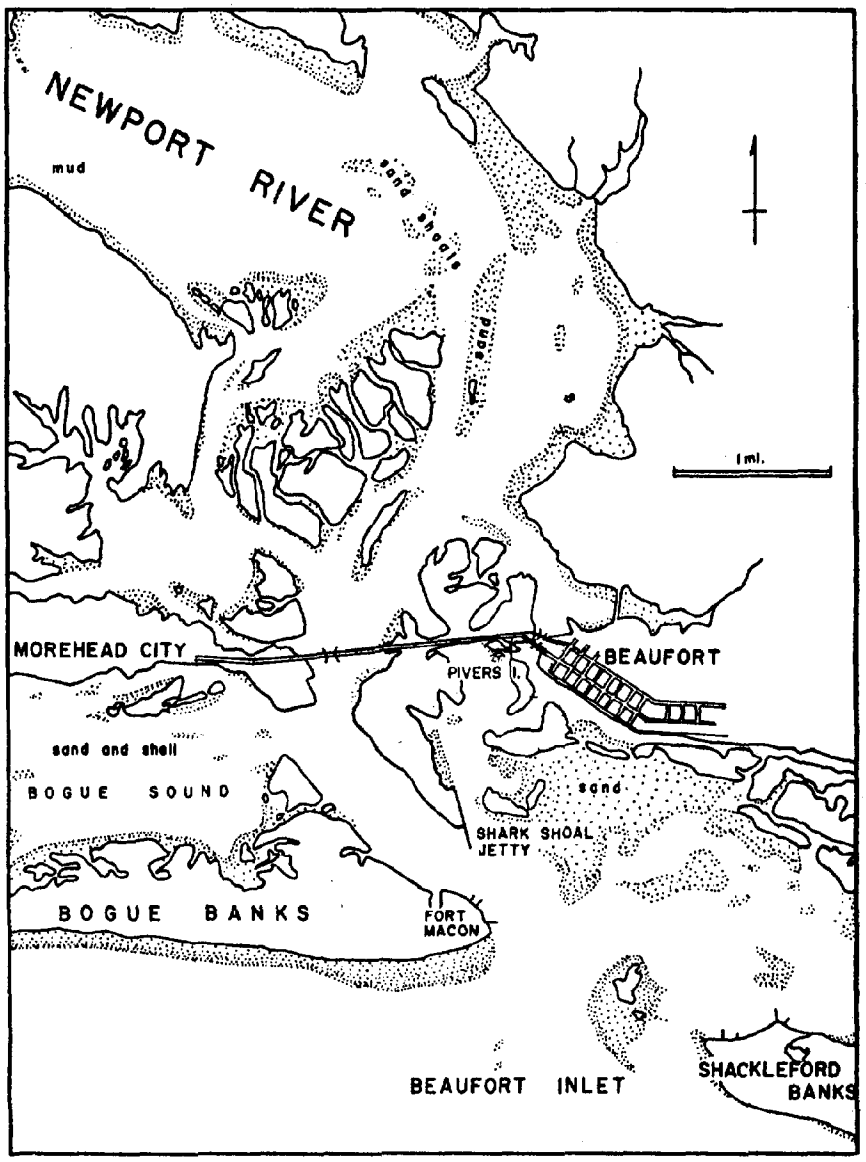


Fig. 15. Map of Beaufort, North Carolina, and vicinity, with notations on the bottom types. (From Maturo 1957).

in mudflats there are given in Figs. 16, 17 and 18. Williams and Thomas (1967) provide biomass data for different substrates (Tables 4 and 5). A food chain diagram for the whelk Busycon, a carnivore on these flats, is shown in Fig. 19.

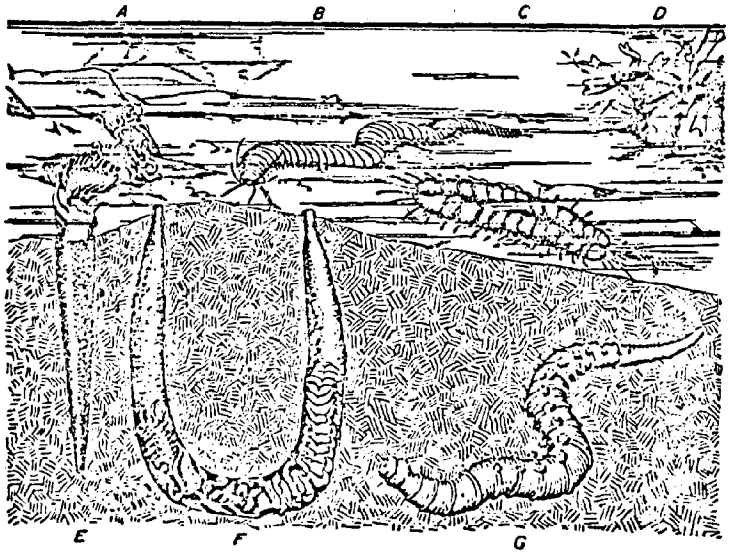
Flats Affected by Sewage

In Fig. 20 is a map of bottom animals of Biscayne Bay, Florida relative to a sewage outfall, and similar patterns are found in San Francisco Bay (Fig. 21).

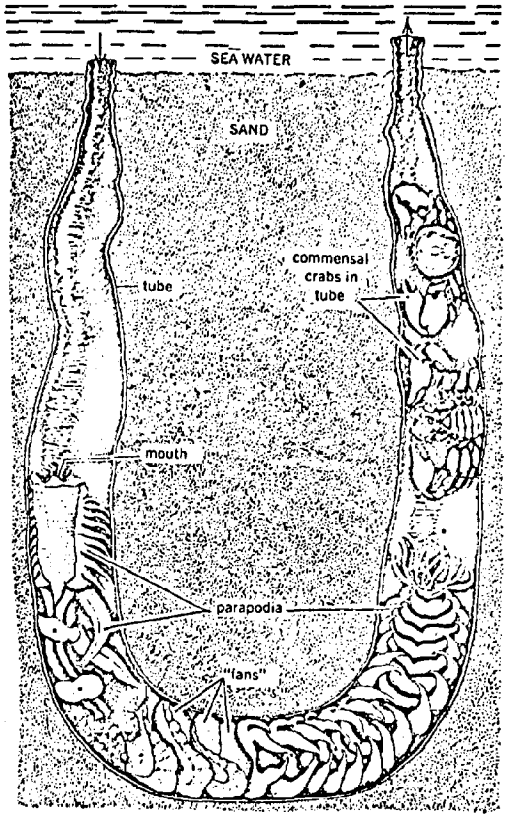
ADAPTATION FOR LIFE ON THE FLAT

As has been pointed out, an exposed intertidal flat in an estuary appears to the uninitiated to be rather barren and almost devoid of animal life except for gulls and terns resting along the fringes, and sand pipers and willets probing into the substrate. Most human visits to a flat are made in mid-day and when the tide is out. These are times when intertidal activity is at its lowest and few species are visible. A visit to the same flat when it is covered with water shallow enough for the bottom to be clearly visible and yet deep enough to float a small flat-bottomed boat, either at night or just after daybreak, will reveal many signs of activity not obvious on an exposed flat. Sea anemones, sea cucumbers, and certain polychaete worms (such as Amphitrite) may have their tentacles fully expanded at the surface; castings from elongated hemichordate worms (Balanoglossus or Saccoglossus), large polychaete worms (Arenicola), and the delicate sea cucumber Leptosynapta are piling up to form conspicuous fecal mounds; brachyuran crabs and hermit crabs are scurrying over the surface in search of food; bivalve molluscs have their siphons expanded; horseshoe crabs, rays, and flounders are groveling in the substrate for food; whelks may be caught in the act of laying eggs or preying on large bivalves; snails are leaving trails through the substrate as they actively move along, or if scavengers, feeding on a dead fish or crab; small fish that invaded the flat with the incoming tide are nibbling in areas recently disturbed by larger animals. In short, the flat comes to life when it is again inundated. However, even then, without digging beneath the surface, one sees only the larger and more conspicuous species.

The major portion of the fauna of a flat consists of infaunal burrowing species that spend most of their lives in the substrate rather than on the surface. Soft bottoms and shifting sand present difficulties for sessile animals and few are able to survive in this kind of environment, except in areas where there are rocks, wrecks, or other firm substrate suitable for attachment. The few sessile animals that attach to the shells of hermit crabs and the carapaces of horseshoe crabs, are of minor importance in the economy of an intertidal flat. On the other hand, the burrowers are numerous, both in number of species and number of individuals, and represent many major groups of marine animals.

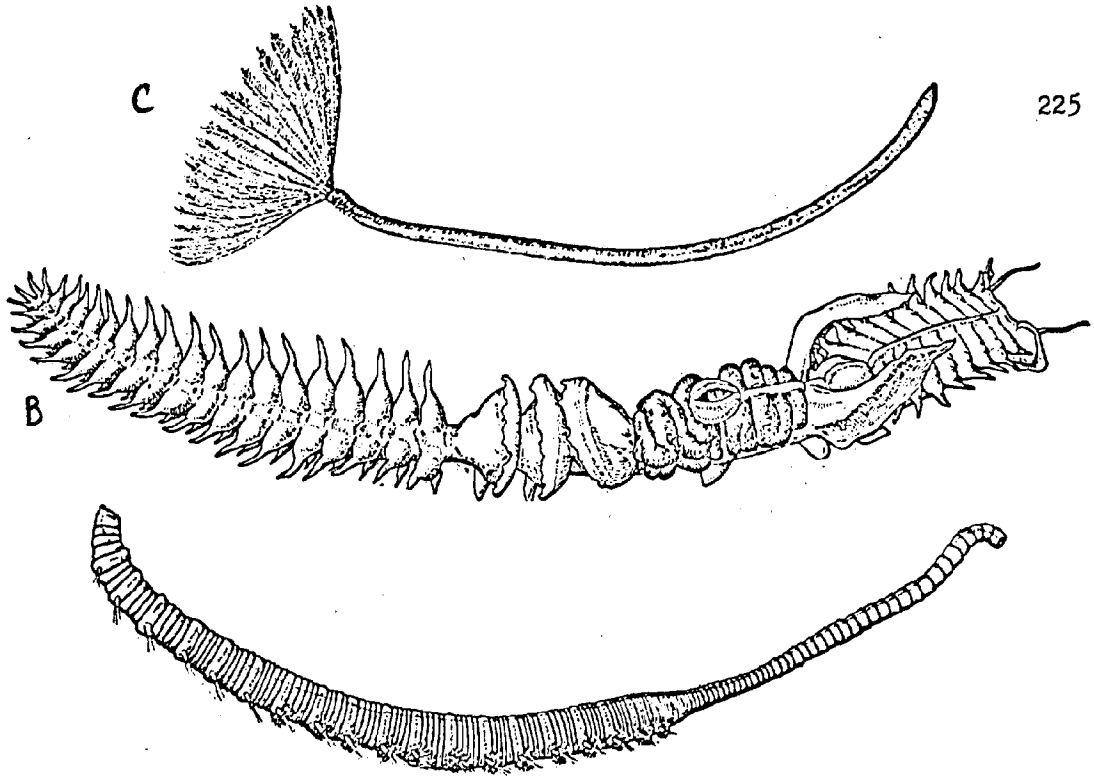


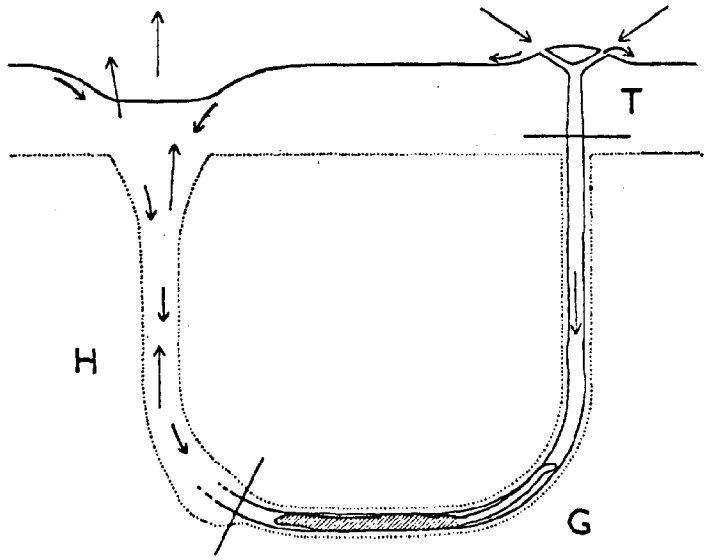
–Marine annelids on sea bottom. Some burrow through the mud, others make tubes of leathery secretions, sand grains, bits of seaweed or lime, which are buried in the mud or attached to rocks, piles, and seaweeds. A, *Hydroides* in calcareous tubes on a rock; B, *Nereis*; C, *Polynœ*; D, *Spirorbis* on seaweed; E, *Cistenides* in sand tube; F, *Chætopterus* in leathery tube; G, *Arenicola*.



Class POLYCHAETA. *Chaetopterus*, a specialized worm dwelling in a secreted tube in the sea bottom. The "fans" are modified parapodia that draw water through the tube. Commensal crabs (*Polyonyx*) also inhabit the tube. (*After Pearse*, 1913 **b**).

Fig. 16. Marine annelids typical of the intertidal flats of the Beaufort area (From Pearse 1929).

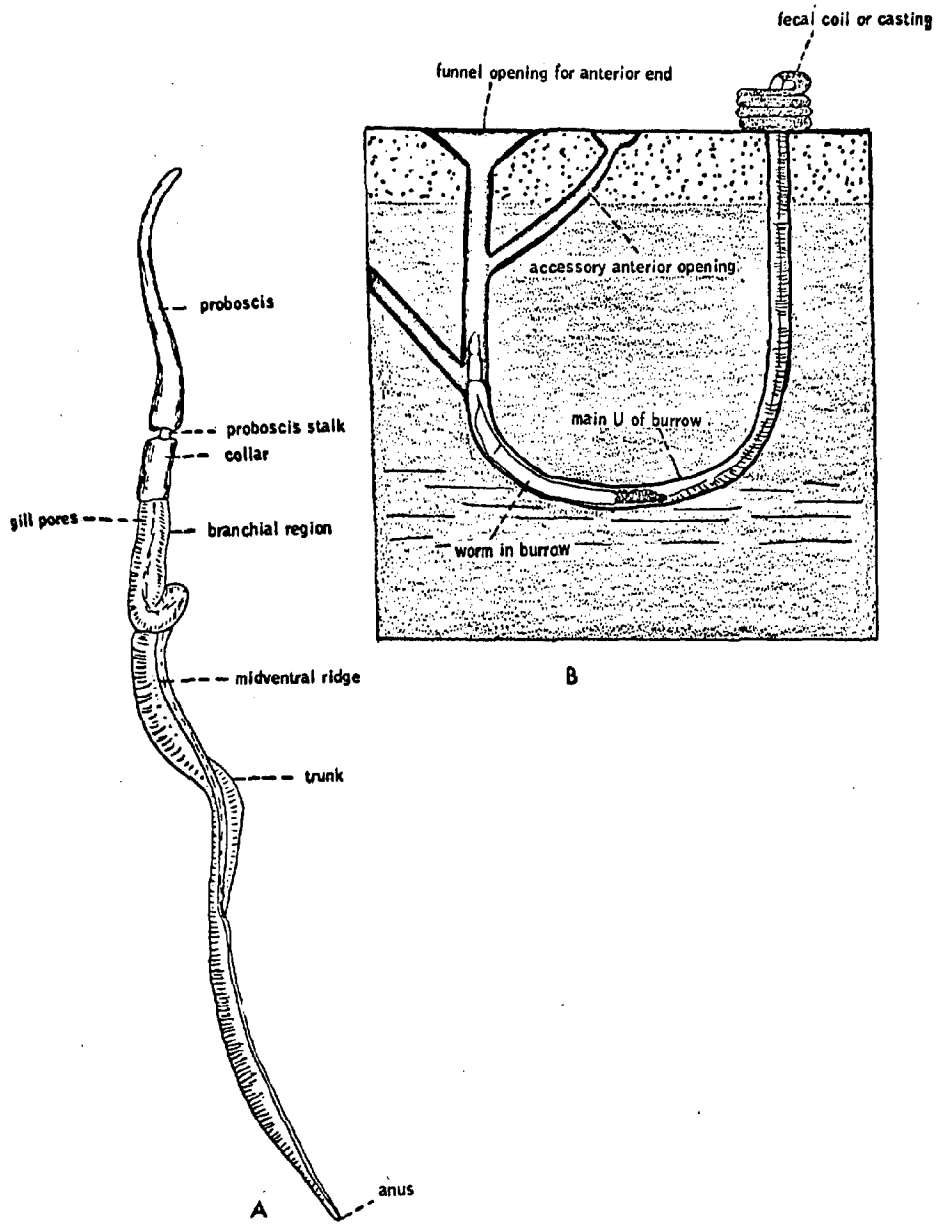




Generalized diagram of a lugworm burrow, with the worm lying quietly in the gallery. The cross lines are drawn at the boundaries between head shaft (*H*), gallery (*G*) and tail shaft (*T*). The dotted line is the boundary between yellow and black sand. The long, thin arrows show the movement of water, and the short, thick ones that of sand.

Fig. 17. Marine annelids of the Beaufort area: A. the lugworm, Arenicola marina (bottom) and its burrow. B. Chaetopterus (See Fig. 16 for secreted tube). C. the feather duster worm, Sabella pavonina (From Wells 1945, 1959; Fig. 10).

PHYLUM HEMICHORDATA



A. Saccoglossus kowalevskii, an acorn worm common to the Atlantic Coast of North America
B. Burrow system of the Mediterranean *Balanoglossus clavigerus.* (After Stiasny from Hyman)

Fig. 18. Acorn worm found on worm flats in the Beaufort area (Saccoglossus). Burrow of Mediterranean worm shown in B. (From Barnes 1968).

Table 4

Standing crop of benthic animals adjacent to Pivers Island, Beaufort, N. C.

Elevation Number	Distance above mlw (m.)	Sediment	Range of values for 355-cm.² Samples		Number (/m.²)			Live Weight (g./m.²)			Decalcified Dry Weight (g./m.²)		
			Number	Live Weight (g.)	Mean (Arithmetic)	Mean (Log)	Confidence Limits*	Mean (Arithmetic)	Mean (Log)	Confidence Limits*	Mean (Arithmetic)	Mean (Log)	Confidence Limits*
1	0.6	Sand	0–4	0–.84	28	19	3–45	2.6	.51	0–2.0	.28	.06	0–.25
2	0.3	Muddy sand	0–6	0–2.06	90	79	44–130	20	6.5	1.5–27	2.0	.79	.23–3.0
3	0.0	Muddy sand	2–9	<.01–17.48	124	111	75–162	50	2.9	.5–13	5.1	.45	.08–2.1
4	–0.6	Muddy sand with grass	3–115	<.01–40.82	672	371	158–825	294	47	7.6–280	32	5.0	.79–30
5	–1.2	Soft mud	0–6	0–3.48	48	35	11–73	13	3.1	.3–14	1.1	.25	.06–1.1
1–5					192			77			8.1		

*95% confidence limits for the mean of the logarithmic values.

(Williams and Thomas, 1967)

Table 5

Dry weight of benthic animals as a percentage of live weight

	Per cent
Crustacean*	
Barnacle	8%
Isopod	16
Decapod	20
Hermit crab (with shell)	5
Mollusk*	
Gastropod	10
Pelecypod	7
Echinoderm*	
Brittle star	10
Sea urchin	8
Tunicate	
Styela plicata	11
Annelid	20

*Decalcified prior to drying.

(Williams and Thomas, 1967)

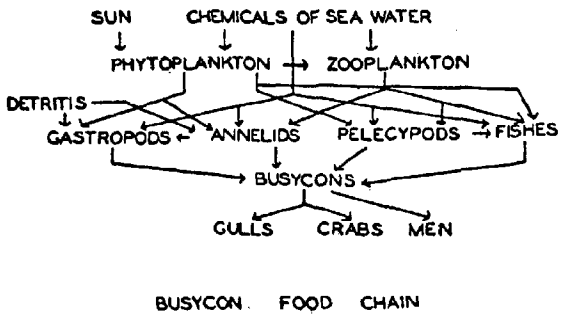


Fig 19. A food chain based on observation of Busycons at Beaufort, N.C. (Magalhaes 1948, Fig 61).

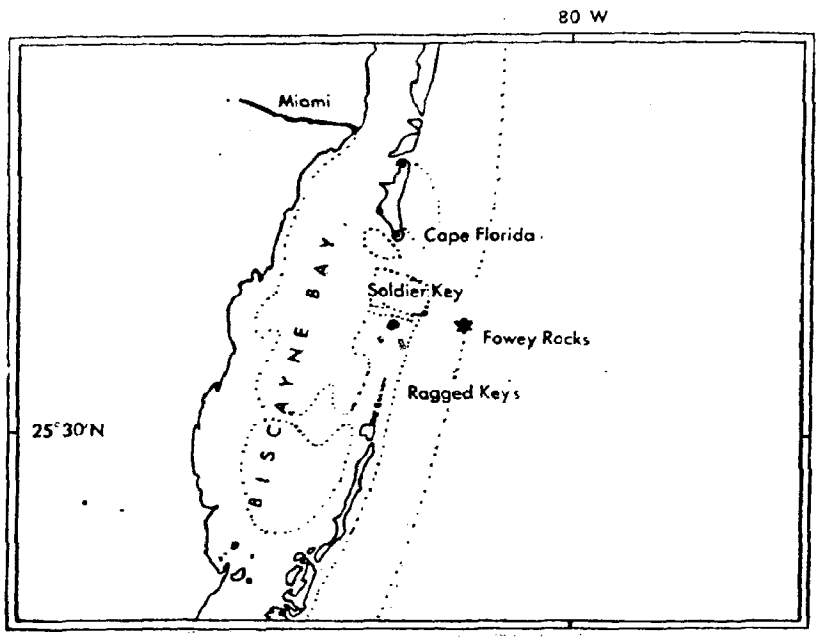
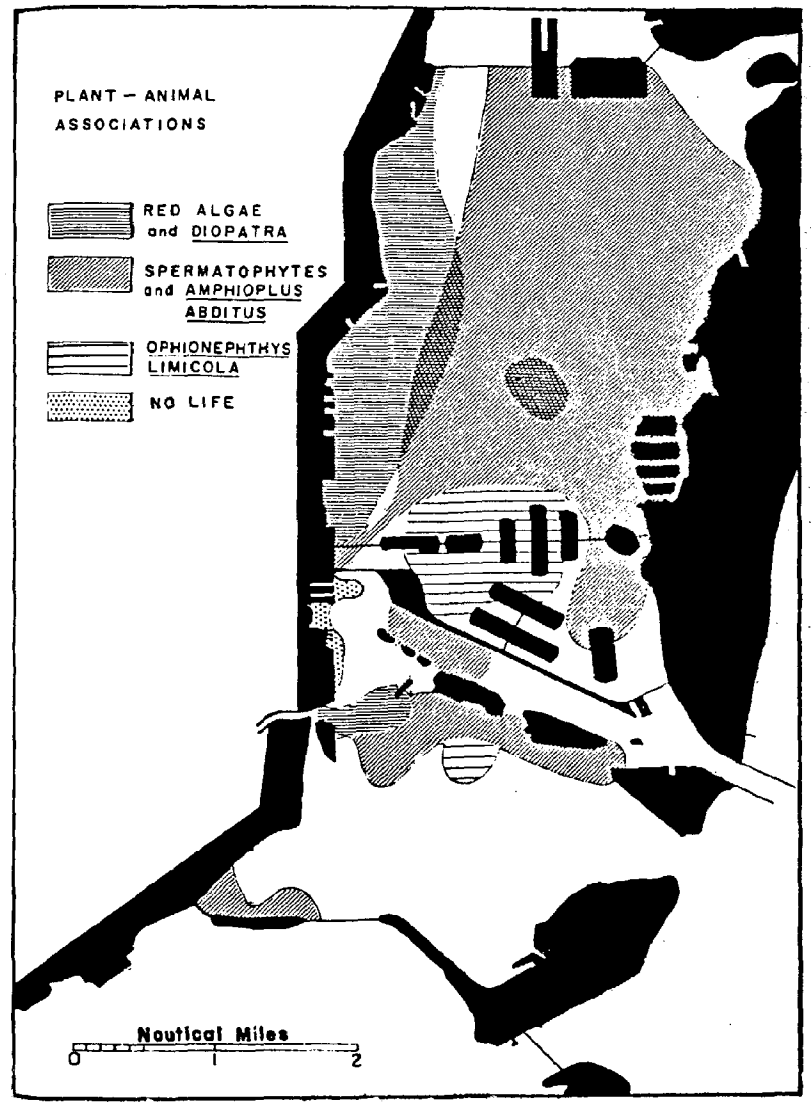
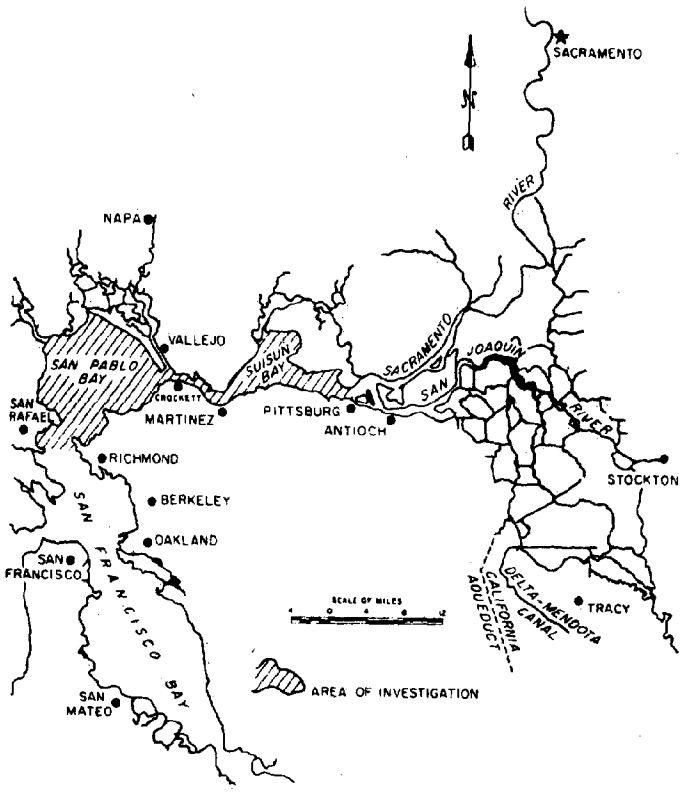


Fig. 20a. Map of Biscayne Bay, Florida (Voss and Voss, 1955).



Horizontal distribution of four benthic biological zones (diagrammatic).

Fig. 20b. Biscayne Bay, Florida and bottom associations (McNulty, 1961).



1.—AREA OF INVESTIGATION IN SAN FRANCISCO BAY SYSTEM

Fig. 21. Map of San Francisco Bay (From Bailey, McCullough, and Gunnerson 1966).

The number of small organisms in the substrate of an intertidal flat is tremendous. Each gram of substrate may contain 500,000 bacteria, thousands of diatoms, and other algae, nematodes, copepods, ostracods, amphipods, etc. (Pearse, Humm, and Wharton 1942). Small organisms require less living space than do large ones and can afford to be more numerous. The abundance of one-celled plants in the substrate cannot be estimated with the naked eye. Some are only a few microns in diameter, but there may be many species and they may occur in exceedingly large numbers. Hustedt (1955) found 369 species of diatoms belonging to 63 genera in two small mud samples (See Fig.22).

It is difficult to compare faunal densities from data taken on various surveys by different authors, for there is a lack of uniformity among investigators in sampling techniques and objectives, and the tabulations are not always limited to the intertidal region alone. Often the total fauna, including that below the low tide mark are lumped together. However, in all cases it is obvious that the polychaete annelid worms, the crustaceans, and the molluscs predominate. This is true for the intertidal flats as well as for the subtidal regions. The following table shows the percentages of species in these three groups in three different New England areas. The first is for intertidal species only; the other two include subtidal shallow water species.

	Polychaeta	Crustacea	Mollusca	All other groups
	%	%	%	%
Barnstable Harbor, Mass. (Fig. 1) (Sanders et al, 1962)	34	23	23	20
Greenwich Bay, R. I. (Fig. 12) (Stickney & Stringer, 1957)	33	22	28	17
Sheepscot Bay, Maine (Hanks, 1956)	47	11*	32	10

* Identifications of Crustacea incomplete.

Benthic invertebrate species differ in size, number of individuals, total biomass of the population, and total food consumption, and therefore vary in their individual ecological importance in the community. Few animals reach the population size of the small bivalve, Gemma gemma. This little clam rarely reaches a length of 5 millimeters but is very abundant as already mentioned for Barnstable Harbor, Mass. It may burrow in the sand to a depth of one or two centimeters. Bradley and Cooke (1959) reported Gemma gemma to average about 38,000 per square meter in Sagadahoc Bay, Maine. The maximum population density there was 289,000.

The distribution of fauna on intertidal flats is not uniform and is sometimes discontinuous (Stickney and Stringer 1957). The reasons for the irregularities are not always apparent, but usually are associated with such factors as type and stability of substrate, strength of currents, wave action, and salinity. While some species live well in either sand or mud substrates,

others have decided preferences, as judged by the density of populations. The polychaete annelids Cistenides (See Fig. 16) and Clymenella build tubes of finely sorted sand grains and are to be found only on the sandy substrates. The polychaete Amphitrite builds its tube of mud and is at home in a mud flat. Two common sea anemones have different preferences: Cerianthiopsis secretes a several-layered parchment-like tube that extends 45-50 centimeters into the mud; Paractis has no tube but expands its base as a holdfast in sand. The short razor clam Tagelus, abundant in mud, decreases in population density in the transition zones of sandy mud and muddy sand. The hard clam Mercenaria, common in mud and the transition zones, is less numerous in sand. The soft clam Mya and the long razor clam Ensis are primarily sand dwellers. Among echinoderms, their means of locomotion prevents most of the members of this group (starfishes, heart urchins, and sand dollars) from living in mud, but the sea cucumber Thyone is often very abundant in mud flats. Many other examples of diversity in substrate preference could be cited. (See Figs. 7, 8, and Table 4.)

Usually mud flats are farther up in the estuary than are sand flats, and occur especially where currents with low rate of flow permit detritus to settle to the bottom. Although mud flats are richer in organic matter, nevertheless sand flats, where currents are not too strong, also accumulate detritus, and harbor equivalent numbers of species. The fact that flats are subjected to alternate wetting and drying with the changing tides, does not mean that the burrowing and tube-dwelling organisms of the infauna are subjected to desiccation when the flats are exposed. The fauna retreat to lower levels in the substrate where water content is higher and temperatures lower in summer and higher in winter than at the surface. Mud flats drain more slowly and are commonly exposed for shorter periods of time than sand flats. Rarely, even at the surface, do they become dry. Sand flats, made up of particles of larger grain size, drain quickly at the surface but retain considerable moisture content a few centimeters down. Uneven sand flats often contain numerous tide pools at low water. Neither mud flats nor sand flats, even though often very extensive in acreage, are much above sea level at low water. Temperature decreases rapidly with depth on the flats in summer, and may be several degrees lower a few centimeters deep than at the surface. For example, when mid-day temperatures in tide pools on a Beaufort flat registered 35° C., the maximum temperature in twelve Chaetopterus tubes was only 29° C. (Gray 1961). Ability to live within the substrate means that a large portion of the fauna of intertidal flats is not significantly affected by tidal, diel, and seasonal changes in climate. This makes for relatively stable communities. Except for Arctic and Antarctic regions, where the severity of winter temperatures reduces the fauna able to survive in intertidal areas, there is considerable uniformity in the types of animals of the flats, although the number of species and number of individuals may vary under special conditions.

The most stable benthic community, according to Thorson (1957), is one in which the whole set of animals is long-lived, and without pelagic larval stages. Long life would insure an overlap of generations and thus reduce the fluctuations in populations. The young would live in the same areas as their parents. Such communities normally exist only in Arctic and Antarctic coastal waters and in the deep sea. As the tropics are approached,

the percentage of benthic species with pelagic developmental stages increases, and in tropical shallow waters reaches its highest value, as high as 85 to 90 percent (Thorson 1950). Sessile fauna are the most stable, but these are insignificant on sand and mud flats. Deeply burrowing sedentary animals, such as the soft clam Mya and the polychaete Chaetopterus, are important elements in the community stability. The shallow burrowers— Echinocardium, Mercenaria, Nucula, etc.--also have relatively stable populations. These endure the major fluctuations in environmental conditions throughout the year.

Most species that have burrows extending ten or more centimeters into the substrate keep outlets open at the surface and have special organs for creating currents for respiration (See Figs. 16, 17, and 18). Some of the larger polychaetes build substantial tubes which permit up and down movement and at the same time prevent the substrate from caving in on the worm. Some build tubes of mud (Amphitrite), some of parchment (Chaetopterus, Diopatra), some of sand grains (Clymenella, Cistenides), and some have no organized tube, but move freely through the substrate. Linings of unknown composition strengthen the extensive burrows of the burrowing shrimp, Callianassa and Upogebia, and prevent collapse. Long-necked clams (Mya and Tagelus) burrow deeper than do short-necked ones, and are capable of sliding up and down in the burrows. Clams with short siphons (Mercenaria) stay near the surface.

FOOD

Sanders et al (1962) recognize five categories of benthic feeding types: 1. Deposit feeders, 2. Suspension feeders, 3. Scavengers, 4. Carnivores, and 5. Omnivores. As is to be expected, considering the nature of the environment, the largest and most characteristic is the basic deposit feeding group. Among the polychaete annelids, (one of the most abundant groups of animals) the smaller and most numerous representatives are largely deposit feeders, living on detritus and diatoms and other single-celled algae. Polychaetes of intermediate size ingest filamentous algae in addition; and the larger species which take animal food as well, must be considered omnivores.

Deposit feeders consume not only detritus but also living diatoms and dinoflagellates, large populations of which live on or near the substrate surface. Moul and Mason (1957) obtained values ranging from 50,000 to 900,000 cells per square centimeter for the top depth of 2.5 centimeters of sediment in the Barnstable locality. The whole plant population, the primary producers of the substrate, was found to be concentrated in three centimeters of sediment. Obviously the benthic diatoms and dinoflagellates are more readily available to the fauna that feed on them than their planktonic counterparts in the waters above.

Chlorophyll values in the substrate of Barnstable Harbor flats average 420/ mg/m^2. This is in sharp contrast to the values for the open water of bays and estuaries (15 mg/m^2) or the waters over the continental shelf (2.5 mg/m^2) (Sanders et al 1962). The deposit feeder is as common in sand as in softer sediments. Its distribution is better correlated with chlorophyll concentration

than with the total organic content of the substrate. Presumably the deposit feeders are utilizing primarily the abundant supply of diatoms and dinoflagellates at the sediment surface. Marine diatoms are shown in Fig. 22. The sediment must be considered as an indicator of food availability and not as a prime factor directly determining the feeding types. Deposit feeders are largely absent from areas where there are ripples, because the unstable sediment surface prevents unicellular algae from becoming established. In intertidal flats where the standing crop of microscopic plants occurs on the surface of stable sediments, both sand and mud, deposit feeders are the dominant feeding type (Sanders et al 1962). The great abundance of diatoms and chlorophyll in the substrate indicate that associated deposit feeders serve a very important function as primary consumers.

The immediate sources of organic detritus in the substrate range from dying and decaying plants and animals and solid excreta from animals inhabiting the waters, to organic debris from nearby terrestrial areas. Except in estuaries well supplied with benthic vegetation, the organic detritus is largely supplied from phytoplankton. The importance of chlorophyll is the transfer of light energy in photosynthesis is no less true of the phytoplankton of the sea than of green plants on land. The phytoplankton, in which diatoms (Fig. 22) and dinoflagellates predominate, are the most important marine producers, although in estuaries where sea grasses are extensive, these plants are also important. Detrital chlorophyll must be produced continuously from dying and decaying phytoplankton and from fecal matter from zooplankton. In the classification of food sources it is probably of minor importance to distinguish between chlorophyll from living and that from dead organisms as long as chlorophyll is available (Jorgensen 1966). Photosynthesis proceeds on an enormous scale through chlorophyll-bearing plankton cells, and it is natural to expect that regions of high organic content will support extensive and diversified populations of organisms. The organized (living) and the unorganized (detritus) organic matter exist in a kind of dynamic equilibrium. Still, in any reasonably stabilized locus the mass of accumulated, standing crop of unorganized detrital material must exceed that of the aggregate of living organisms (Fox 1957). Detritus particles are generally associated with bacteria engaged in decomposing the organic substrate, and these may also serve as food for the detritus feeders. According to Jannasch (1958) bacteria may be as much as 5,000 times more abundant on the bottom than at the water surface, but it is quite probable that the bacteria associated with detritus serves a greater function as decomposers of the detritus than as food.

The potential sources of food for suspension feeders (such as clams) are classified into convenient groups by Jorgensen (1966): phytoplankton; suspended particulate dead organic matter (detritus); dissolved or colloidal organic matter; heterotrophic organisms (bacteria, fungi, yeasts, and certain flagellates); and zooplankton, which themselves consist mostly of suspension feeding organisms, including planktonic larvae of many benthic animals, but which also may serve as food for larger suspension feeders.

The types of feeding organs adapted to suspension feeding are numerous and varied, but nearly all make use of flagellated chambers or ciliated

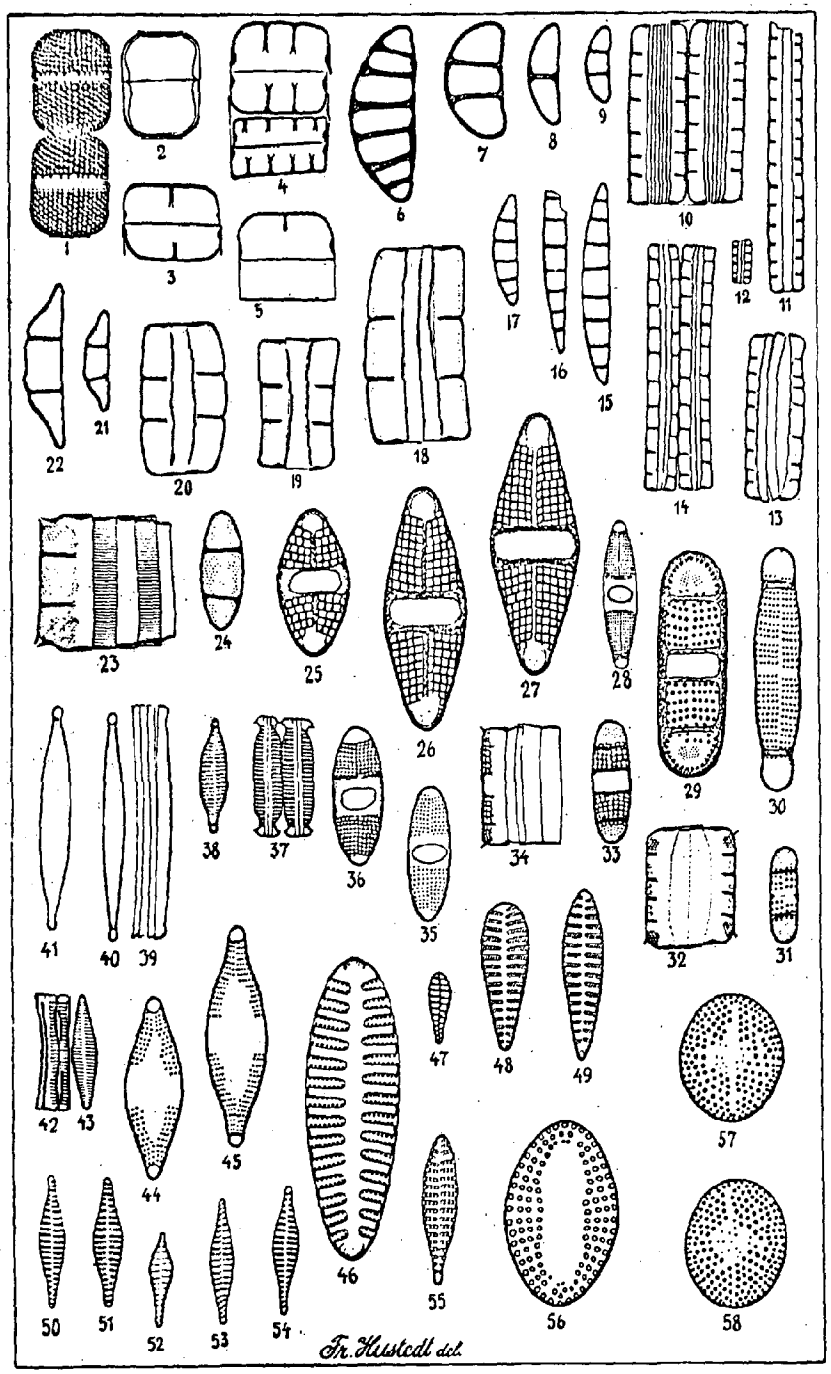


PLATE 4

1, 2. *Melosira Hummii* nov. spec. (see pl. 1, f. 3-5)
3-9. *Eunotogramma laeve* Grun.
10-17. *Eun. marinum* (W. Sm.) Per.
18-22. *Eun. rostratum* nov. spec.
23, 24. *Anaulus americanum* nov. spec.
25-27. *Plagiogramma rhombicum* nov. spec.
28. *Pl. tenuistriatum* Cl.
29. *Pl. Wallichianum* Grev.
30-34. *Pl. pygmaeum* Grev.
35, 36. *Pl. staurophorum* (Greg.) Heib.
37, 38. *Dimerogramma rostratum* nov. spec.
39-41. *D. hyalinum* nov. spec.
42, 43. *D. acutum* nov. spec.
44, 45. *D. maculatum* (Cl.) Freng.
46. *Opephora Schwartzii* (Grun.) Petit
47-49. *Op. pacifica* (Grun.) Petit
50-54. *Trachysphenia acuminata* Per.
55. *Tr. australis* var. *rostellata* nov. var.
56. *Rhaphoneis surirella* var. *australis* Petit.
57, 58. *Rh. grossepunctata* nov. spec., the two valves of the same frustule.

Magnif. 1000/1.

Fig. 22. Diatoms of the marine littoral region of Beaufort, N.C. (From Hustedt 1955).

areas for water transport. Most feed by passing the surrounding water through filters that retain suspended particles. In others, the water with its suspended particles is carried along surfaces capable of retaining the particles. Secretion of mucus is of importance in this. The mucus is passed by ciliary action to the mouth.

Tremendous amounts of water pass through populations of suspension feeding bivalves. From water containing an average of five mg of suspended material per liter, the bivalves filter tons and tons of potentially nutritive material each year. Less than five per cent of the ingested material is incorporated into the tissues (growth); the rest is used in metabolic activities. The significant fraction that is voided finds its way to the substrate, there to enrich the supply of food for the numerous deposit feeders (Fox 1957).

Suspension feeders generally constitute a well-defined group, but there are often difficulties in delimiting the group from other feeding types, especially when the difference in size between the consumer and its food is very small. Suspension feeders among the benthic epifauna obtain their feeding current from the water masses that often have re-suspended bottom materials. However, many suspension feeders that live more or less buried in the bottom may take their food from water immediately above the bottom. The suspended material in this case may originate from stirred up bottom matter, so the food conditions of these forms are not directly comparable with those of typical epibenthic suspension feeders. These are deposit feeders.

Together detritus feeding and suspension feeding represent the most common types of feeding among the infauna of intertidal flats, and perhaps of the epifauna also. These two feedings types are basic in the food webs of benthic communities of sand and mud flats and are widespread among different groups of marine invertebrates: sponges, coelenterates, annelids, brachiopods, urochordates, hemichordates, cephalochordates, crustaceans, molluscs, echinoderms, echiuroids, polyzoans, and the pelagic larval stages of benthic fauna.

The relation of feeding type to sediments in the intertidal zone differs from that in the subtidal regime where the infaunal suspension feeder is present in large numbers in well sorted sand, and the deposit feeder is most common in sediments high in silts and clays (Sanders 1958). Subtidally the primary source of food is from the water column. The plant cells and detritus that sink to the bottom accumulate on soft sediments where currents are weak. Because of this the deposit feeders are the characteristic feeding type on finer sediments. Suspension feeders are widely distributed and abundant in well sorted sand of intertidal islands. However, where rippling is pronounced the sediment is so unstable that the suspension feeders here, as in the subtidal region, become reduced in numbers.

Since both deposit feeders and suspension feeders are, at least in part, primary consumers, it probably makes little difference which predominates in

the ecological economy of the food web. One or the other, or both types, are essential in that the all-important single-celled plants of both the phytoplankton and of the substrate, the initial energy converters, are consumed.

Although the number of species among the primary consumers--deposit and suspension feeders--is large, the number of species that occur in significantly large populations is relatively small. Only a few are constant dominants, that is, appearing is sizeable populations in practically all flats; and only approximately 25% can be considered major elements in terms of biomass.

Some deposit feeders cycle large amounts of sand through their alimentary tracts, deriving nourishment from adsorbed particulate matter. The large (up to 30 cm in length) lugworm Arenicola has an eversible proboscis for burrowing through the substrate. When feeding, mucus is secreted and this entraps sand and organic matter. A great deal of indigestible material is passed through the alimentary canal and at intervals evacuated to the surface in the form of castings. The large hemichordate Balanoglossus and the smaller Saccoglossus feed in much the same way as does the annelid Arenicola, and their castings are conspicuous on sand flats where these species occur abundantly. The similarity in structure of the burrows of the h michordates and Arenicola are apparent in Figs. 16-18. The diameter of the casting of Balanoglossus may be as much as two centimeters. The slender sea cucumber Leptosynapta, an abundant and wide spread genus, also ingests sand and mud for the organic matter of the detritus. In comparison to Balanoglossus and Arenicola its castings are rather delicate (MacGinitie and MacGinitie 1949).

Another abundant polychaete, Clymennella torquata, constructs a vertical tube from fine sand grains cemented together with mucus. The tube protrudes a few centimeters above the substrate surface. The worm, head downward, ingests sand and detritus at the bottom of the tube and passes fecal matter out the free end. In this species Mangum (1964) found latitudinal variations in population sizes and amount of substrate turnover per year as follows:

	Maximum Population Size No./m^2	Turnover ml/yr
Beaufort, N. C.	180	365
Barnstable Harbor, Massachusetts	610	136
Passamaquoddy Bay, New Brunswick, Canada	675	96

The figures suggest that although the populations of this species are smaller in milder climates, the active feeding season is much longer. At best, however, the maximum substrate turnover is very small compared to the tons cycled each year by the much larger Arenicola and Balanoglossus.

The larger burrowing shrimp of the flats also feed by sifting the substrate for microscopic organisms. Two of the more common ones are Callianassa major and Upogebia affinis. The former makes extensive burrows in sand as much as 60-190 centimeters deep, with openings to the surface (Pohl 1946). On the other hand, the latter makes its burrows 30-50 centimeters deep in muddy substrate (Pearse 1945).

In the trophic levels above the primary consummer are the predators, both carnivores and omnivores. These are not as numerous as the primary consumers, but may be much larger and consume vast numbers of those at the lower level. The horseshoe crab (Limulus) preys on clams, heart urchins, polychaetes, and other burrowers which it obtains by groveling in the substrate. Horseshoe crabs although not rare, are not abundant on the flats except in the spring egg-laying season. Some snails (Eupleura, Urosalpinx, Polynices) feed upon bivalves and other snails by drilling holes in the shell and then consuming the defenseless prey. Whelks, of which there are several species, exert pressure on the shells of the larger bivalves and insert the edge of their own shell between the valves until the clam opens. Whelks are not limited in diet to bivalves; they also feed on annelid worms, gastropods, and dead fishes and other animals. Whelks are among the dominant animals of the intertidal flats (Magalhaes 1948). A diagramatic food chain as it affects the whelks is shown in Fig. 20. It is typical of the food chains of intertidal flats, regardless of the predators involved. All food chains have at their base the primary consumers. Secondary consumers are varied.

The efficiency of energy transfer in ecosystems is very low. Energy fixed by green plants is almost completely dissipated after passage through three or four consumer species; thus food chains must of necessity remain short. Furthermore many consumer species do not stick to one particular trophic level in feeding. Alternate foods may--perhaps must--be used from time to time (Darnell 1961).

In the previous pages an attempt has been made to present a picture of the normal community relations, including the relative abundance of organisms and their positions in the food web, of a typical undisturbed intertidal flat. The primary producers--in this case the numerous species and multitudinous individuals of diatoms and dinoflagellates of both the plankton and substrate--are fed upon by the primary consumers, the deposit feeders and the suspension feeders of which the former are particularly numerous. The primary consumers are in turn fed upon by a variety of omnivores and carnivores that constitute the predators of the flats. If left to themselves the various organisms of the intertidal community largely control their own population sizes.

PROPERTIES OF THE SEDIMENTS

Deposition of sediment is a characteristic of estuaries, and its rate far exceeds that in the ocean. The bulk of the sediment of most estuaries is contributed by rivers. The most characteristic and best known estuarine substrate consists of clays and silts and organic matter, and is found principally in the upper reaches and quiet lateral branches of estuaries (Carriker 1967). Nevertheless, admixture of sands and coarser particles occur in the direction of the inlets and wave exposed shallow and intertidal zones. Bottoms under strong currents and wave action may be predominantly sand (Day 1951). According to Carriker (1967) estuarine sediments and waters are characterized by specific and complex physical, chemical, and microbiological properties, interactions and interdependencies which together constitute a unique estuarine environment for benthic animals. This estuarine biotope is thus not a simple

overlapping of factors extended from sea and from land, but a unique set of its own factors arising within the middle reaches from materials contributed by the surrounding environments. The finest sediments are in the quieter waters and the heaviest near the entrance to the estuary. Much of the latter is derived, not from rivers, but from erosion of beaches and from the sea floor, the materials being brought in by incoming tides or severe storms (Emery, Stevenson and Hedgpeth. 1957).

Reworking of the sediment goes on constantly within the estuary, particularly on the shallow flats where tidal currents erode and redeposit the sediment. In a healthy estuary many burrowing animals aid in reworking the substrate, bringing up materials from underneath to the surface. The well known study of Charles Darwin many years ago (1890) established that burrowing land animals, such as earthworms, are very effective in mixing the uppermost layers of the soil. In shallow estuaries this function is carried on by many species and it is now apparent that mud-feeding animals play a significant part in reworking the sediment. Preliminary unpublished data indicate that a single acorn worm (Balanoglossus aurantiacus) may turn over as much as 550 grams of substrate per day. This is a very common species on the sand flats of the southeastern United States. Deposition and reworking of sediments are normal events in an estuary. The turnover of substrate reduces anaerobic conditions, permits aerobic bacteria and oxygen to enter the sediments. This enables decomposition to continue with the subsequent return of phosphates, carbon dioxide and ammonia to the substrate surface and waters above, where these can again be used by the producers.

In shallow waters interface reactions appear to be overwhelmingly dominated by bacteria, and when aerobic conditions prevail aerobic bacteria increase in numbers (Hayes 1964). The chemical nature of the humus must of necessity take into consideration its origin from bacterial decomposition of plant and animal residues, often preceded by animal digestion. Anderson (1939), summarizing the work of others, particularly Waksman (1933), points out that the organic matter of the marine bottom has a characteristic chemical composition, similar in many respects to the humus in soils of field and garden. The organic matter is not inert, but can undergo slow but gradual oxidation. In shallower bottoms and close to land, organic matter is oxidized more readily than in the depths of the sea. A detailed discussion of the chemical complex of estuarine sediments has been made by Nelson (1962), and reviewed by Carriker (1967).

Anaerobic bacteria can also carry on decomposition, but under anaerobic conditions, as in mud and heavily silted areas, the rate of decomposition and the return of nutrients to the waters above are very slow. The presence of oxygen is essential for rapid decomposition of marine humus. Oxygen, however, is a conspicuous variable at the underwater substrate interface. Under some conditions there may be seasonal depletion in summer. On the other hand, turbulence created by currents, wave action and agitation of the substrate, renews oxygen at the interface. Oxygen by itself does not penetrate deeply into fine substrates. Kanwisher (1962) states that oxygen penetrates only one or two millimeters in organically rich habitats such as salt marshes, and except on an open ocean beach he found no indication of oxygen below one

millimeter in other situations examined. Oxygen does penetrate deeper, however, where there is turnover of the substrate by animal activity. It is below the burrowing layer that the decline in numbers of aerobic bacteria with depth begins.

EXPORT TO WATERS ABOVE

Fishery biologists have long recognized the role of bottom dwelling animals as food for commercially important fishes and crabs. In fact, the success of many fishery operations depends on the quantitative distribution of forage organisms that live on and in the substrate. There are many thousands of square miles of fishing waters in the numerous sounds that connect to the ocean through inlets (Carson 1944). Such commercial species as shad, striped bass and herring pass through these sounds at spawning time, and sea trout, mullet, croakers, blue crabs and oysters normally abound in them. Mullet in their seasonal migrations often invade the deeper reaches of brackish water estuaries. These are bottom feeders. Sea trout often live a large part of their lives in estuaries where they feed on crustaceans and small fishes. The young of black drum remain within estuaries until reaching a length of four inches or more. These feed largely on shellfish. Estuaries are important nursery grounds for shrimp in spring and summer, before they move into open ocean waters later. Blue crabs, far more abundant in estuaries than in the open ocean, are of great commercial importance in the mid-Atlantic, southeastern and Gulf states.

Talbot (1966) emphasized the value of the estuary as a nursery and feeding area for striped bass, an important fish for food as well as for sport. It feeds directly on bottom dwelling animals such as polychaete worms, crustaceans, and molluscs, as well as on small fishes and crustaceans which are themselves bottom-feeders. The importance of bottom animals to ducks was shown by Harmon with data in Table 6.

Saila (1961), on the basis of extensive tagging of juvenile populations of flounders in estuaries, found that 25% of the total recruits to the offshore flounder fishery of Rhode Island were contributed by shallow lagoons, thus emphasizing the importance of shallow water estuarine environments. Saila's (1962) tagging experiments in one portion of Narragansett Bay also showed that flounders in model hurricane barriers were able in a relatively short time, to find their way through openings, and thus the barriers did not act as physical impediments to the fish that use the bay for spawning or feeding.

SOURCES OF STRESS

Natural Phenomena

At times nature may make sudden and drastic changes in an estuary. A hurricane may create new inlets or close old ones, affecting the circulation of water; it may cause sand to cover mud or marsh; excessive rains may decrease the salinity to such an extent that the waters of the estuary temporarily become

fresh causing the death of much of the sessile fauna. But natural disturbances, violent as they may be, that reduce salinity in an estuary to the fatal limits of tolerance of the fauna, are usually not of serious consequence in the long run since recovery is rapid. Many biotic communities recover fully in a year or two. Wells (1961), while studying the seasonal changes in the fauna associated with oyster reefs in the Newport River Estuary, North Carolina, had his work interrupted by a series of three hurricanes in one month. At the more inland stations the water remained fresh for so long that most of the marine organisms succumbed. But as this is a tidal estuary, and as most of the benthic fauna have planktonic larval stages, repopulation began as soon as the waters returned to more normal salinity; this was almost immediately for species still in their breeding season, later for those that had passed their breeding period, and almost a year later for some species. Repopulation by larvae brought in by the tide was essentially completed in a relatively short time and little or no permanent damage resulted. This example is typical of recovery from sudden but temporary natural disturbances of the environment where the substrate itself is not seriously and permanently modified. Disturbances of this type are only temporary disasters. But disturbances caused by filling of marshes and shallow water ways, pollution by excessive raw sewage and industrial wastes, and excessive use of insecticides that drain into the estuaries may have serious permanent effects on the natural cycling in the ecosystem, and recovery may be impossible.

Silting

One of the greatest difficulties with which bottom fauna have to contend is the filling of bays and estuaries. Silting has been on the increase and many formerly productive bottoms along the Atlantic and Gulf coasts have been destroyed or reduced in their efficiency by high rates of sedimentation. Sanders (1958) found in Buzzards Bay, Massachusetts, that sediments consisting predominantly of silts and clays support meagre populations of filter-feeding organisms--clams, oysters, etc. These sediments reflect the feeble currents which permit the fine particles, including the organic matter, to settle out. Striped bass eggs for example, heavier than water, require water movements to keep them suspended. If not suspended they settle, become silted over, and have small chance of survival. There is a smaller amount of organic matter in suspension under these conditions for filter-feeders. Filter-feeders are more abundant where there is a well-sorted grain size and stability of substrate, whereas in muddy substrates deposit-feeders predominate, making up 80 to 99 percent of the fauna. Spotfin killifish, croakers, and other bottom feeders have greatly diminished in the Chesapeake Bay area due in large part, apparently, to silting of the bottom.

A small scale example of the effects of excessive sedimentation occurred in recent years at Beaufort, North Carolina. Dredgings from a boat channel were piled high on the far side of an adjacent island near a tidal drainage from an extensive nearby shoal. Rains and winds carried silt from the dredgings on to the flat faster than the tidal current could carry it away and in a few months three to five inches of silt covered the sandy intertidal substrate.

This smothered the adult animals, and as the new substrate was unsuitable for larvae to settle on, new populations could not get started and the area became barren. After a year or two, when the source of the silt was reduced, currents carried away much of the deposited material and repopulation of the flat began. Unfortunately, loose sediments drained from the flat into another section of the channel, and to overcome this the engineers completely closed the tidal drainage outlet from the flat. Now, the second year after halting tidal drainage with circulation of water greatly impaired, silting has increased and the fauna is again disappearing.

Where the rate of silting is low some of the bottom fauna may be able to adjust to the gradual filling in, but when silting occurs faster than the animals can adjust, they soon become smothered and the area becomes restricted to minute silt-loving species.

Heated Effluents

The effects of heated effluents on benthic species is quite variable, depending on latitude and whether there are oxidizable materials accompanying the heated water. Viewpoints vary as to whether it is desirable to suppress the fauna affected, or to encourage its production. Naylor (1965a,b) has reviewed the effects of heated effluents. High temperatures are often associated with low concentrations of oxygen, and some animals, the polychaete Hydroides for example, show reduced tolerance to high temperatures in the presence of low oxygen. With high temperatures one would expect the elimination of cold water stenothermal species. The edible blue mussel, Mytilus edulis, a cold water species that extends southward along the east and west coasts of the United States until it reaches summer water temperatures too high for it to tolerate, is an example. In estuaries with hot water effluents it is easily eliminated, since it is a sessile animal and cannot avoid the unfavorable conditions. In the Delaware River estuary there has been an almost complete elimination of fishes from the maximum heated regions in summer. Probably the fish migrate to cooler regions, but many of the benthic invertebrates are not able to avoid the excessive temperatures. Many species are attracted to temperatures up to 26 to 28° C., but the number that can survive above 32° C. is greatly reduced, and all are eliminated at temperatures of 40- 43° C. On the other hand, heated water in estuaries permits some sub-tropical species to become established farther north than they would normally live. Many species have ranges of temperature above or below which they fail to breed and thus, depending on conditions, are encouraged or hindered in becoming established in an estuary. In southern California, heated effluents have been used in reducing fouling organisms (Fox and Corcoran 1957). In high latitudes many species live at temperatures far below their upper limits of toleration and readily survive heated effluents. In tropics and sub-tropics species already living close to their upper limits of heat toleration cannot stand increased heated water. Markowski (1960) found that near the heated outfall of a power plant in England, the ten degrees higher temperature made it more favorable for some species than near the intake. No algae grew at the intake, but there was prolific growth at the outfall. However, coelenterates and polyzoans did better near the intake, perhaps because of the lower velocity of the water.

It would seem then that heated effluents, without toxins or oxidizing materials, may or may not be disastrous to the bottom fauna of an estuary, depending on latitude and other factors.

Sewage Effects

Biscayne Bay, Florida

McNulty (1961) has pointed out that the most harmful effects of sewage pollution, at least in Biscayne Bay, are limited to within 200 yards of the sewage outfalls. Here the bottom is characterized by sticky mud having a high content of oxidizable organic matter. In shallow water with good circulation and firm sandy bottom, there is an increased abundance of individuals of benthic animals 200 to 600 yards from sewage sources.

Sewage pollution is very damaging to the estuarine shellfish industry. The filter-feeding oysters, clams, and quahogs retain some of the bacteria taken in while feeding. In most coastal states propagation of shellfish must meet the standard of not more than a coliform bacterial median of 70/100 ml of water. In North Carolina alone it has been necessary to prohibit the taking of shellfish in 44,000 acres due to contamination.

San Francisco Bay

Felice (1959) compared polluted areas with normal areas in San Francisco Bay. He dredged bottom materials from 312 stations in a tributary entering the bay and found a distortion of normal fauna in various pollution categories. Close to sewer outfalls, where pollutants are maximum, the substrate is almost devoid of life. At a distance, where estuarine waters dilute the waste, animal life does exist. Although a marginal habitat open to only a few benthic animals,the species that are tolerant grow in large numbers. The parts of the estuary that contain clean unpolluted water support many species. His results may be summarized as follows:

1. Normal Bottom: Thirty-nine species averaging 6.5 species per liter of substrate. Twelve species in this habitat were not found in areas exposed to wastes.

2. Maximum Industrial Pollution (at outfalls): Three species at an average of one per ten liters of substrate. Only one small crab, *Rithropanopeus harrissii*, has high tolerance for this environment. Seventy-five percent of the stations were without fauna.

3. Marginal Industrial Pollution (downstream where wastes are diluted by estuarine waters): Twelve species at an average of three per ten liters of substrate. *Rithropanopeus harrissii* and the polychaete *Nereis succinea* occurred in large numbers and seemed indifferent to the environment. Forty-three per cent of the stations were without fauna.

4. Maximum Domestic Pollution (at the outfalls): Five species at an average of two per ten liters of substrate. *R. harrissii* and the polychaete *Capitella capitata*, an indicator of pollution, occurred in larger numbers than expected. Fifty per cent of the stations lacked fauna.

5. Marginal Domestic Pollution (downstream where wastes were diluted and adsorbed on silt): Thirty species with an average of 11.5 species per ten liters of substrate. Of the species that occurred here, 77% were in greater density than at the other habitats, and only three stations were without fauna. Except in number of species, this habitat compared favorably with the normal environment.

Table 6. Bottom animals as duckfood in low salinity waters off Louisiana (Harmon, 1962).

TOTAL POUNDS OF MARINE ORGANISMS PER ACRE FOUND OFF-SHORE OF ROCKEFELLER WILDLIFE REFUGE IN THE GULF OF MEXICO

Distance from shore	Mulinia lateralis*	Nassarius acutus	Nuculana concentrica	Hemipholas elongata	Neanthes spp.	Total
100 feet	0	0	0	0	0	0
500 feet	0	2.94	0	0	0	2.94
1/4 mile	0	7.34	0	0	0	7.34
1/2 mile	12.24	0	1.59	0	0	13.83
1 mile	9.42	4.41	0	0	10.64	24.47
1 1/2 miles	7.34	23.50	0	0	0	30.84
2 miles	22.40	1.47	1.59	0	0	25.46
2 1/2 miles	119.95	8.81	3.31	8.93	0	141.00
3 miles	88.49	1.47	0	0	5.75	95.71
4 miles	272.94	14.69	1.59	40.02	0	329.24

*Traces of other marine organisms which showed up in the sampling were Retusa canaliculata, Pinnixia sp., Epitonium rupicolum.

Identification of marine organisms by Donald Moore 1961.

TEMPERATE GRASS FLATS

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INTRODUCTION

There are a number of flowering plants which have returned to the sea from land via fresh-water (Cromie, 1966; Moldenke, 1940; Scagel, 1961). All species are placed in the Class Monocotyledonae of the Division Anthophyta. The total accepted number of described species varies with the author, but counts vary from 34-35 (Setchell, 1920) to almost 50 (den Hartog, 1964, 1967; Moldenke, 1940).

There are few parts of the world where one or more species of seagrass have not adapted. Seagrasses, as a plant type, are dominant growth forms and demonstrate patterned distribution (Carriker, 1967). Moore (1958) stated that the seagrass community, whether it is Zostera in the north temperate region or Thalassia in the tropics, is an entity, distinct and recognizable, wherever it is found. Thus, it forms a system.

Tropical and subtropical regions contain the greatest number of species. In temperate regions the number of species diminishes. In temperate North America, including the Atlantic and Pacific coasts, five species have been reported. One, Halodule wrightii Aschers., just reaches the temperate zone in North Carolina. Two species, Phyllospadix scouleri Hooker and P. torreyi Watson, are limited to the lower littoral-upper sublittoral fringe along surge beaten coasts on the Pacific coast. Ruppia maritima L. is found along both coastlines in those parts of estuaries with greatly reduced salinity. Simmons (1957) reported Ruppia from the Laguna Madre in Texas in areas with salinities up to 45 0/00, but reports also exist of the species living in freshwater (Humm, 1956; Ostenfeld, 1927). The species probably is of little relative importance as a system in the temperate zone. Wood (1959a, b) stated that leaves in Australia supported few epiphytes and that the plant required good illumination. Thus, the extent of growth of Ruppia in an estuary is usually limited to very shallow water.

Zostera marina L., eelgrass (Fig. 1), forms the single most important north temperate seagrass system. Much has been written concerning this species. Some work has been quantitative; much more has been qualitative. Until the last five years most of the work concerning eelgrass in the United States evaluated the effects of its disappearance during the 'wasting disease' epidemic in 1931 along the Atlantic coast. Much investigation centered on eelgrass in Denmark during the 1900-1930 era. Since 1960 several centers of research dealing with eelgrass have spawned in the United States.

This treatment will tend toward a general analysis of the eelgrass system. Two excellent case histories have recently appeared dealing with the system: McRoy (1966) in Alaska and Burkholder and Doheny (1968) in New York. The latter study was probably done in conjunction with a survey conducted by the Leonard S. Wegman Co., engineers (Wegman, 1967). I will present unpublished data from a study made in Puget Sound.

For a comprehensive bibliography of eelgrass up to 1966, see Phillips (1964) and McRoy and Phillips (1968).

GEOGRAPHIC DISTRIBUTION

On the Pacific coast of North America eelgrass extends from Port Clarence, Alaska (65° N. Lat.; Porslid 1932), as far west as Atka Island (175° W. Long.; Mr. Robert D. Jones, Jr., personal communication), and as far south as Agiopampo Lagoon, Mexico (26°N. Lat.; Steinbeck and Ricketts, 1941).

On the Atlantic coast of North America eelgrass extends from Hudson Bay, Canada, the southern tip of Greenland, and one locality in Iceland (to at least 65°N. Lat.; Ostenfeld, 1918; Cottam, 1934) to Cape Hatteras, North Carolina (35°N. Lat.; Cottam, 1934).

Outside North America eelgrass is found along English coasts, down the Spanish coast, and along the northern Mediterranean coast into the Black Sea (Ostenfeld, 1918). Eelgrass is abundant in Denmark, mainly on the eastern inner coastal side to about 57° N. Lat. It extends into the Baltic Sea and reaches its northern point of distribution in the Aland Sea (ca. 60° N. Lat.; Ostenfeld, 1908). Zenkevitch (1963) reported the species from the White Sea (ca. 65-70° N. Lat.). Eelgrass is found in Japan and in the Yellow Sea from about 32° N. Lat. to the southern tip of the Sakhalin (USSR) (ca. 47° N. Lat.; Miki, 1932).

Eelgrass is a circumhemispheric plant of northern temperate waters. It appears that until more exact collection data are available, the Arctic Circle is the northern point of distribution in all waters.

Two methods of distribution are available, one by detached plants which later reestablish when they come to rest, the other by seed germination. Ostenfeld (1914) stated that detached plants did not live long; however, Conover (personal communication) found that eelgrass plants dangling in a closed system in his laboratory regenerated new roots, leaves and rhizomes. Tutin (1938) stated positively that detached eelgrass plants are usually capable of growth in suitable areas and are apparently an important means of distribution. McRoy (1968) stated that dispersion of the species on a large scale is accomplished through the seed-producing and vegetative plants that annually detach and drift with surface currents. The seed plants could

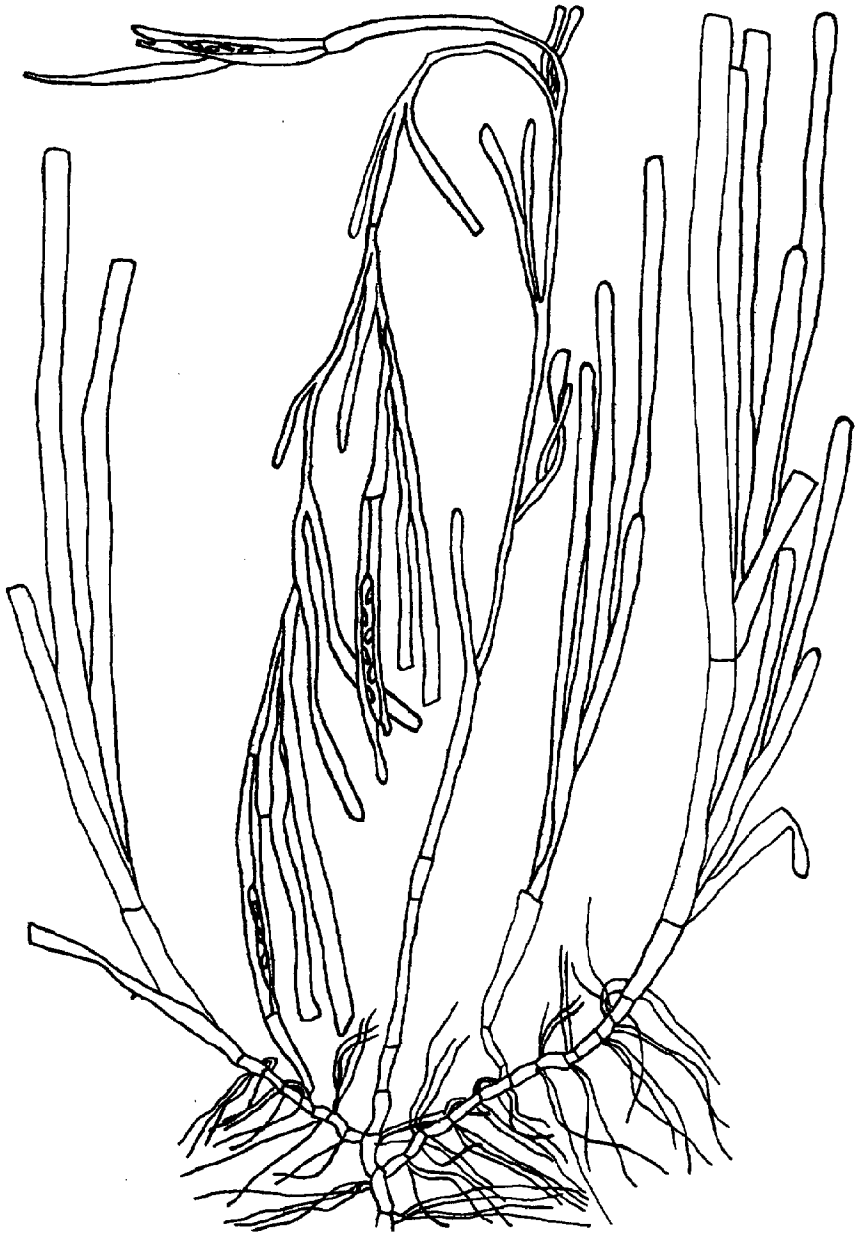


Fig. 1. Eelgrass, Zostera marina L. (after Setchell, 1929). (Note that the terminal leafy shoot, the turion, is fertile; it bears three flowering spathes).

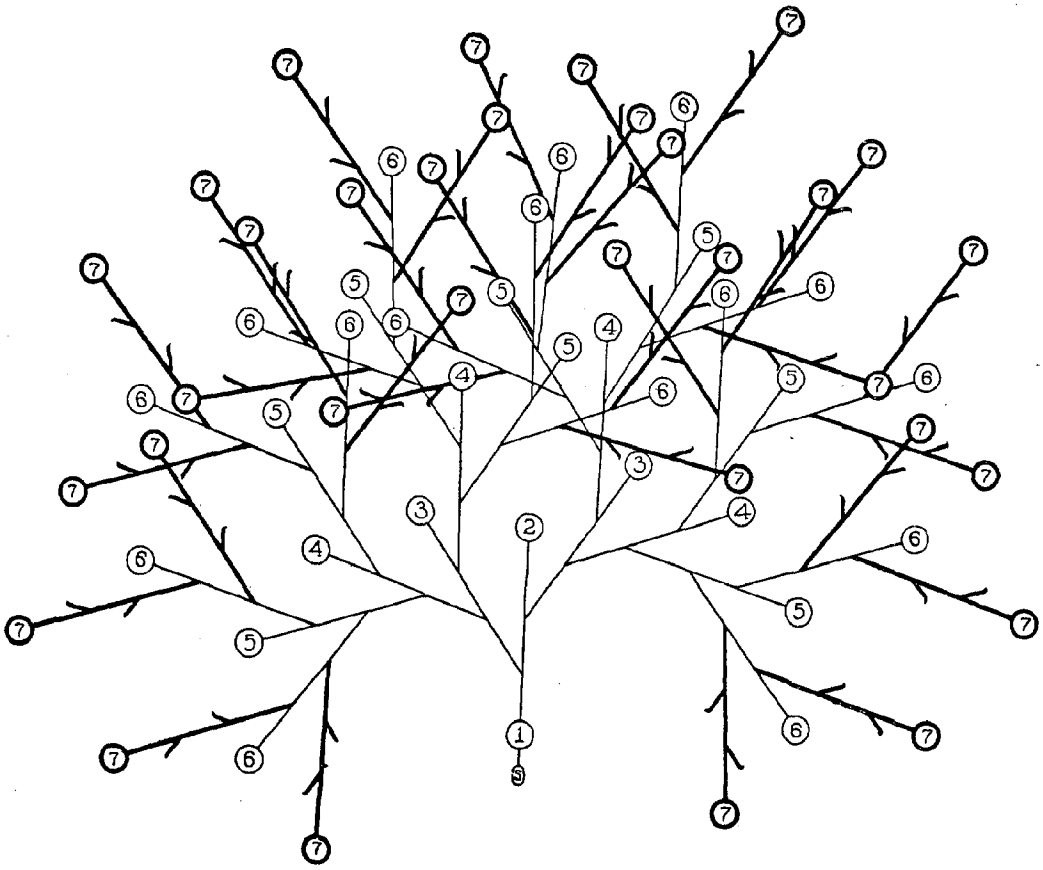


Fig. 2. Diagram of eelgrass branching and fragmenting at beginning of seventh season. Arabic numerals indicate successive terminal buds (or turions). Lateral spurs indicate lateral buds and branches of the season. S indicates the seed. The light lines represent rhizome fragments and plants which have disappeared. The heavy lines represent the living rhizomes and plants. (After Setchell, 1929).

release seeds along their path of circulation. Löve (1963) theorized that Zostera could disseminate by means of floating seeds. Sculthorpe (1967) stated that Zostera seeds either float for only a short while or sink immediately. I have preliminary data which suggests that when seeds become separated from the seed plants by natural means, the seeds immediately sink. When seeds were separated from the seed plant by force, the seeds floated. This experiment was done with both eelgrass and Phyllospadix scouleri Hooker. My data substantiates the statements of both Sculthorpe (1967) and McRoy (1968).

Seeds are eaten by a variety of animals, i.e., ducks and perhaps other marine animals, which could then disseminate them along their travel routes. Ostenfeld (1914) did not believe that seeds could be successfully germinated after passing through the alimentary tracts of marine animals, but Arasaki (1950a) fed seeds to ducks and obtained a high percentage of germination upon recovery of the seeds.

In a local area eelgrass extends its cover principally by vegetative growth from rhizomes (McRoy, 1968). Arasaki (1950b) has shown that a single plant will cover 30 cm.^{2} the first year, one meter^2 the second, and two meter^2 the third. Setchell (1929) diagrammed the manner in which a single plant branches and finally forms an extensive bed of plants (Fig. 2).

In one experiment in Puget Sound in 1964 I denuded one square meter of bottom in a dense bed of eelgrass in the littoral and another meter in the sublittoral. After four months the denuded plot in the littoral had been recolonized by no germinating seeds but contained 10 plants from rhizome extension of neighboring vegetative plants. No plants were found in the sublittoral plot. Germinating seeds were found at this time scattered throughout eelgrass from the littoral to the lowest depth of growth in the sublittoral. After five months the littoral plot contained five young plants from seeds and at least 25 vegetative plants. No plants were seen in the sublittoral plot. When observations on the denuded plots finally ceased after seven months the littoral plot contained at least 50 plants from vegetative rhizome growth and five plants from germinated seeds. The sublittoral plot contained only five plants from vegetative growth. Two conclusions are possible: 1. Grazing pressure on benthic organic matter is heavy in the sublittoral, particularly on a conspicuous denuded plot in the middle of a dense bed of grass, 2. The larger sublittoral plants do not grow as quickly as the smaller littoral plants.

The data in Fig. 3 is after Setchell (1934). I assume that the extreme limits of distribution on the map are diagrammatic.

ECOLOGY OF EELGRASS

Temperature

Eelgrass survives under a wide range of water temperatures. It appears that an overall range of 5°C to 27°C would include most areas where the plant is established. Extreme limits of 0°C (Greenland, Hout 1962) to a substrate temperature of 40.5°C at a depth of 3-5 cm (Japan, Arasaki 1950a)

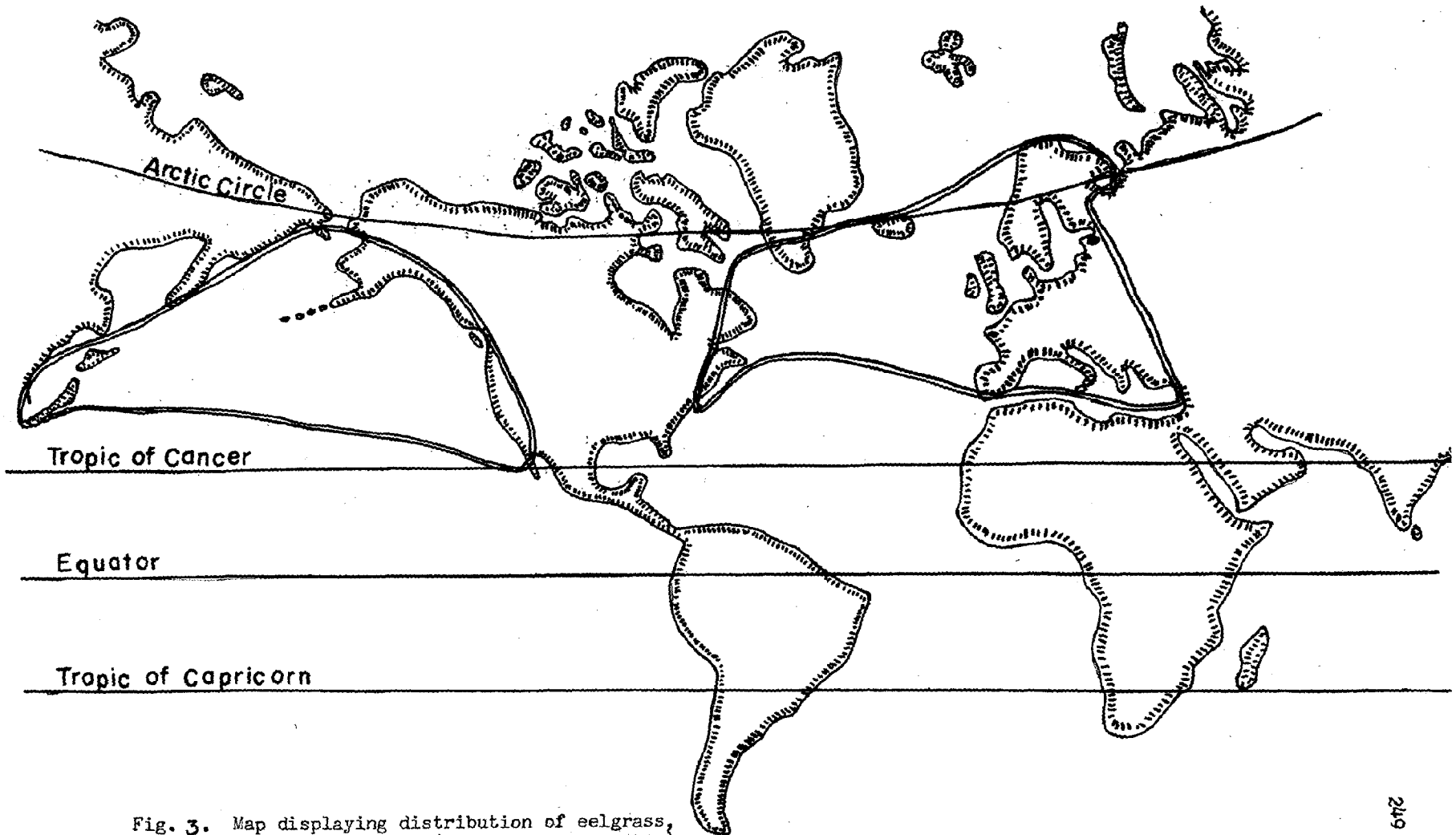


Fig. 3. Map displaying distribution of eelgrass, Zostera marina L. (after Setchell, 1934).

exist. Optimum temperatures for growth seem to lie between 10-20°C in most areas of the world. In Puget Sound, Washington, optimum temperatures range from 7.5°C to 12.5°C. Puget Sound waters ordinarily do not warm beyond the upper limits as listed here. Local higher temperatures up to 18.0°C may occur briefly in Puget Sound proper where tides are sluggish and during daytime summer low tides.

Setchell (1929), after correlating plant activity and rising water temperatures for a number of Atlantic coast stations and one in California, decided that eelgrass displayed five periods of activity governed by 5°C temperature intervals (Figs. 4, 5, 6). The explanation holds that growth and development of eelgrass is controlled by water temperature alone. Setchell (1922) stated emphatically that eelgrass was not dependent on a photoperiod for growth and reproduction.

It is my personal contention that the interaction of light and water temperature has not been properly considered. In Puget Sound eelgrass initiates its vegetative growth in spring at a temperature slightly less than that of the last month of cold rigor. Flowers are initiated at a water temperature well below the 15°C mark as derived by Setchell (near 8-9°C) during April and May, months of increasing day lengths. In Puget Sound there is no heat rigor nor any seeming correlation of plant activity and water temperature. In Puget Sound both intertidal and subtidal plants flower.

In Alaska McRoy (1966) found that tidal pool plants flowered after water in the pools was warmed over 15°C during summer low tides. Subtidal plants did not flower. Water temperatures in the subtidal occasionally warmed up to 15°C in summer. On this basis McRoy accepted the temperature regime of Setchell (1929).

Perhaps eelgrass in the northeast Pacific is physiologically different from that on the Atlantic coast, in California, in Alaska, or in Japan. Research on this aspect would be profitable.

To reiterate, in Puget Sound growth rejuvenation (new leaf and root production) and flower production begin as the daylength increases. Along the Atlantic coast with slower tides and more extensive shallow bays, water would be warmed more by the increasing radiation. Thus, light and water temperature are interrelated and separation of the effects of each is difficult. Hout (1962) stated that the eelgrass in Hudson Bay, Canada, was subjected to a temperature range from 0°C to 4°C , and that applying Setchell's system, the population had to exist in a quiescent state without the ability to propagate. He considered this unlikely, as natural mortality would soon claim the population. Definitive culture work is needed.

Salinity

Eelgrass exists in a wide range of salinity. It is considered to be euryhaline. In Denmark Ostenfeld (1908) considered that a salinity range of 10-30 o/oo was optimum for growth. Arasaki (1950a) reported that eelgrass in Japan grew best in a salinity range of 23.5 - 30.7 o/oo, and that at a salinity of 18.0 o/oo growth was poor. Below 9.1 o/oo growth was checked, although plants did not die.

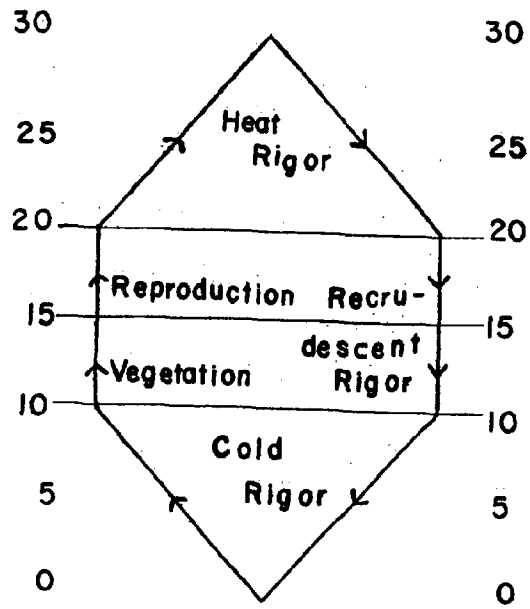


Fig. 4. Pattern polygon representing extremes of temperature conditions of growth and reproduction of eelgrass. Cold rigor - from lowest temperatures experienced to or from 10°C.; vegetative - from 10°C. to 15°C.; reproductive - from 15°C. to 20°C.; heat rigor - from 20°C. to and from the highest temperature experienced; recrudescent rigor - from 20°C. downward to 10°C. (After Setchell, 1929).

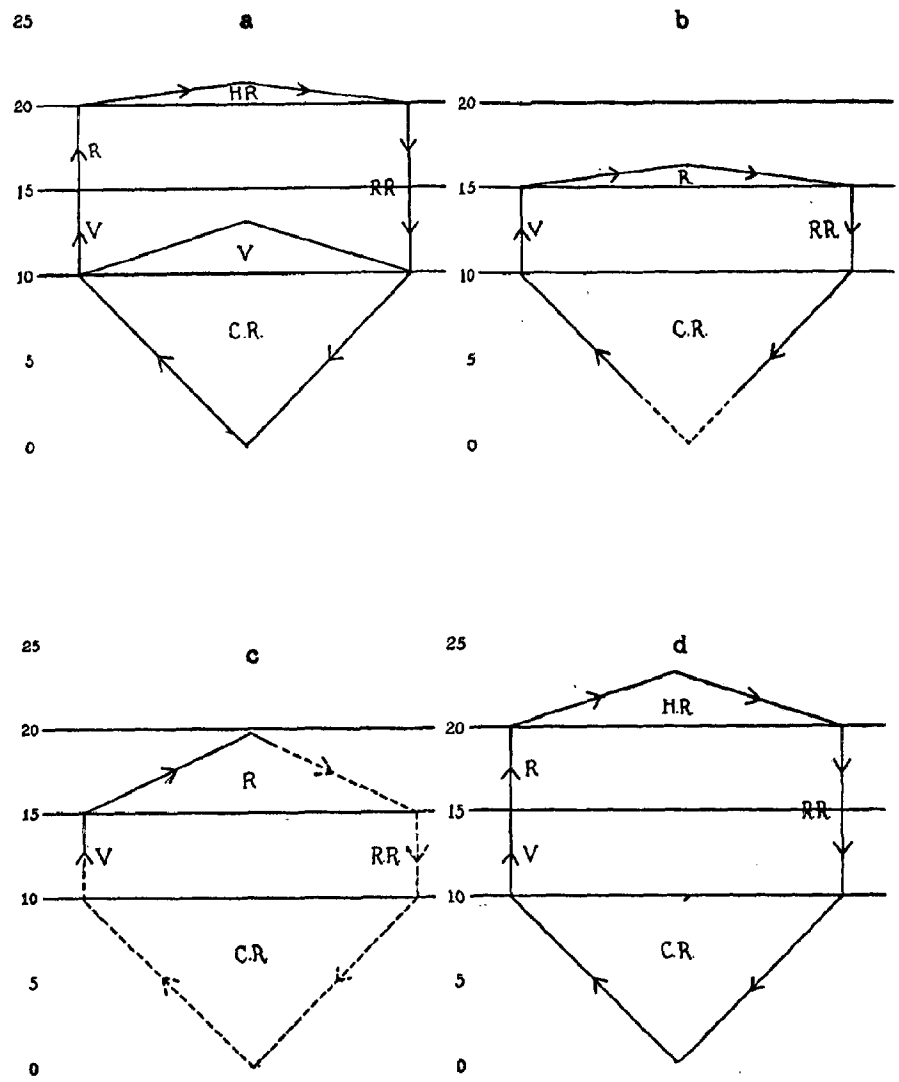


Fig. 5. Polygons representing temperature cycle of localities where eelgrass was collected. V indicates vegetation; R, reproduction; HR, heat rigor; RR, recrudescent rigor; and CR, cold rigor. (After Setchell, 1929).

a. Conditions both above and below extreme low water mark for vicinity of St. Andrews, New Brunswick.

b. Conditions for vicinity of Mt. Desert Island, Maine.

c. Conditions for outer coast, vicinity of Newport, Rhode Island.

d. Conditions for vicinity of Woods Hole, Massachusetts.

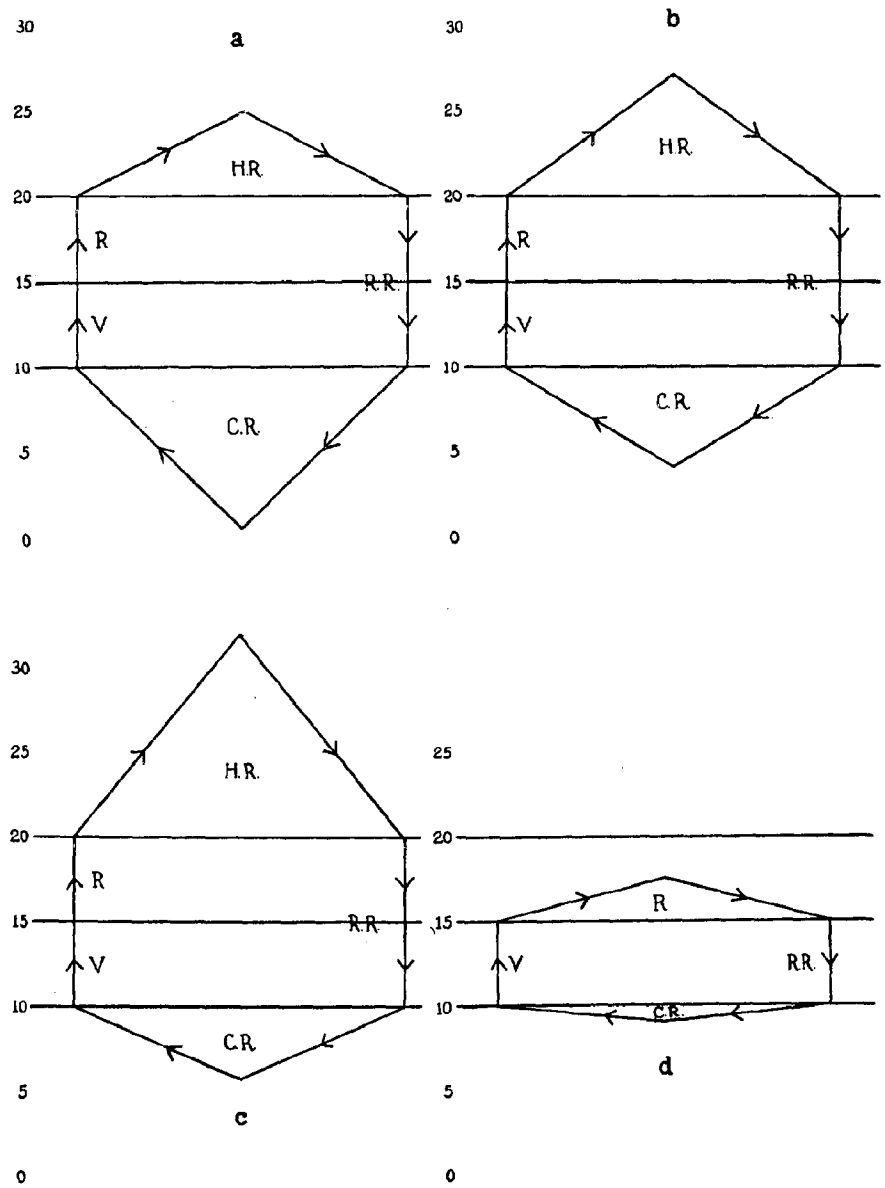


Fig. 6. Polygons and symbols as in Fig. 5. (After Setchell, 1929

a. Conditions at Lees River, Massachusetts.

b. Conditions for vicinity of Barnegat Bay, New Jersey.

c. Conditions for vicinity of Beaufort, North Carolina.

d. Conditions for Paradise Cove, Marin County, California.

Martin and Uhler (1939) found that eelgrass extended upstream in estuaries to a salinity averaging about 25% of normal sea water (ca. 8.5 o/oo). Uphof (1941) reported that Zostera was found along the Netherlands in salinities ranging from 20 - 33 o/oo.

Tutin (1938) stated that eelgrass in an English Bay withstood summer salinities as high as 42 o/oo. In the lab Tutin grew plants for a considerable period in salinities ranging from 10 - 40 o/oo without apparent harm. Plants withstood freshwater for two days. Osterhout (1917) found that at Mount Desert Island, Maine, eelgrass endured and even flourished at the mouths of brooks where alternate changes of salt water and fresh water occurred every six hours. He proposed physiological types of eelgrass, i.e., those which live in marine water and those which have adapted to alternating exposures to fresh water. He conducted experiments on plants from both areas. Protoplasts on leaf cells from marine waters suffered when exposed to fresh water, while those from mouths of streams withstood fresh water for several hours. Osterhout (1917) also found that cells of roots from both areas were killed in several minutes upon exposure to fresh water. He proposed that little change in salinity occurred in the substrate, and that roots did not adapt to fresh water. This lack of adaptation was not due to permeability differences in the membranes of root and leaf cells. Arasaki (1950a) also found a differential reaction of parts of eelgrass to salinity.

In the United States eelgrass lives within the salinity ranges as listed for Europe and Japan.

Arasaki (1950a) reported that salinity had a stronger effect on seed germination than temperature. Optimum salinities for seed germination varied from 4.5 - 9.0 o/oo (60% germination). He reported that light had no effect on germination. Earlier this was stated by Tutin (1938) who also found that acids, bases, and salts had no effect on germination.

Depth and Light

A complex of factors are interrelated in this consideration. An increasing water column results in decreasing light for benthic plants. Substrate and wave exposure are functions of these two factors. A muddy substrate is more easily stirred than is a firm sandy one. Waves would not affect a soft substrate in deep water to the degree as in shallow.

Ostenfeld (1908) found the maximum depth of eelgrass in Denmark to be 11 meters in clear water and 5.4 meters in turbid water. Techet (1906) stated that eelgrass grew to 18 meters in the Trieste Golf. McAtee (1939) reported eelgrass to 14 meters in Holland. Caspers (1957) reported eelgrass depth to 20 meters in the Black Sea. Zenkevitch (1963) recorded eelgrass to six meters in the White Sea. In Japan Arasaki (1950a) stated that the upper limit of growth was 10 cm below low tide. Tutin (1938) noted the lowest limits of growth in England as four meters below their low spring tides. In California Cottam and Munro (1954) stated that dense eelgrass meadows were observed 40 - 50 feet deep (12 - 15 meters) in La Jolla Bay by SCUBA divers, and patches of growth were seen to at least 100 feet (30 meters) on the slopes of the La Jolla submarine Canyon.

In Puget Sound I have determined eelgrass depth as approximately 22 feet (6.6 meters) below mean lower low water (MLLW). This would be approximately 11 meters depth at high tide, and would agree with Ostenfeld's maximum depth from Denmark. Upper limits are difficult to fix. In Puget Sound I have one record at six feet (1.8 meters) above MLLW. The station was heavily shaded by tall trees growing close to shore. Usually, in Puget Sound the upper limit of growth is MLLW. Type of substrate, slope, exposure to sun, and shading are all factors involved in the intertidal occurrence of eelgrass.

A correlation may be drawn with the depth. Phillips and Grant (1965) reported that, as a result of field transplanting, intertidal narrow leaved plants grew wide leaves when placed in the sublittoral, and vice-versa. Ostenfeld (1908) found that leaf width was correlated with firmness of substrate. McRoy (1966) found a correlation between leaf width and plant density and depth of growth, but found no clear gradient of plant characteristics with depth and diminishing light in an Alaskan Bay. In Puget Sound Phillips and Grant (1965) reported a gradient of changing leaf characters in relation to tidal zones.

Substrate

In Denmark Ostenfeld (1908)reported that eelgrass colonized substrates varying from pure firm sand found where wave action was strong to soft mud of quiet bays and fjords. He reported a correlation between leaf size and nature of substrate. On wave exposed coasts with firm sand to the six fathom depth limit of eelgrass, a narrow-leaved plant was found. In sheltered areas two growth forms were recorded: a shallow water narrow-leaved plant on a mixed sand and mud substrate, and a deeper wide-leaved plant on soft mud. He concluded that the length and width of the leaves was more dependent on the substrate than on depth.

Molinier and Picard (1952), working with Posidonia and Cymodocea in the Mediterranean, stated that these two seagrasses would only spread and colonize if organic matter were mixed with sand.

In England Tutin (1938) found eelgrass on a wide variety of substrates ranging from soft mud to gravel mixed with coarse sand. Growth was patchy where exposed to severe wave action with substrates mostly of gravel. The usual substrate was firm muddy sand, often covered with a layer of coarse sand.

Eelgrass existed in extensive stands on sandy clay in the northwestern part of the Black Sea (Caspers, 1957).

McRoy (1966) analyzed substrate composition in an Alaskan lagoon (Figs. 7,8

I have never observed eelgrass growing on pure sand. At a slight depth below the surface (no more than five or six cm) an odor resembling hydrogen sulfide is always found. Boysen - Jensen (1914) found that ferrous sulfide was almost always present in the muddy substrate of eelgrass. Wood (1959a, 1959b), working with Australian species of Zostera, stated that roots were located in a milieu of reduction while the leaves were located in oxidized water. He found Zostera on bottoms of strong oxidizing potential in gravel to strong reduction potential in sand reduced with abundant hydrogen sulfide. He stated that the Zostera normally is rooted in a reducing environment, and that its metabolism was probably adapted to such an environment. He further

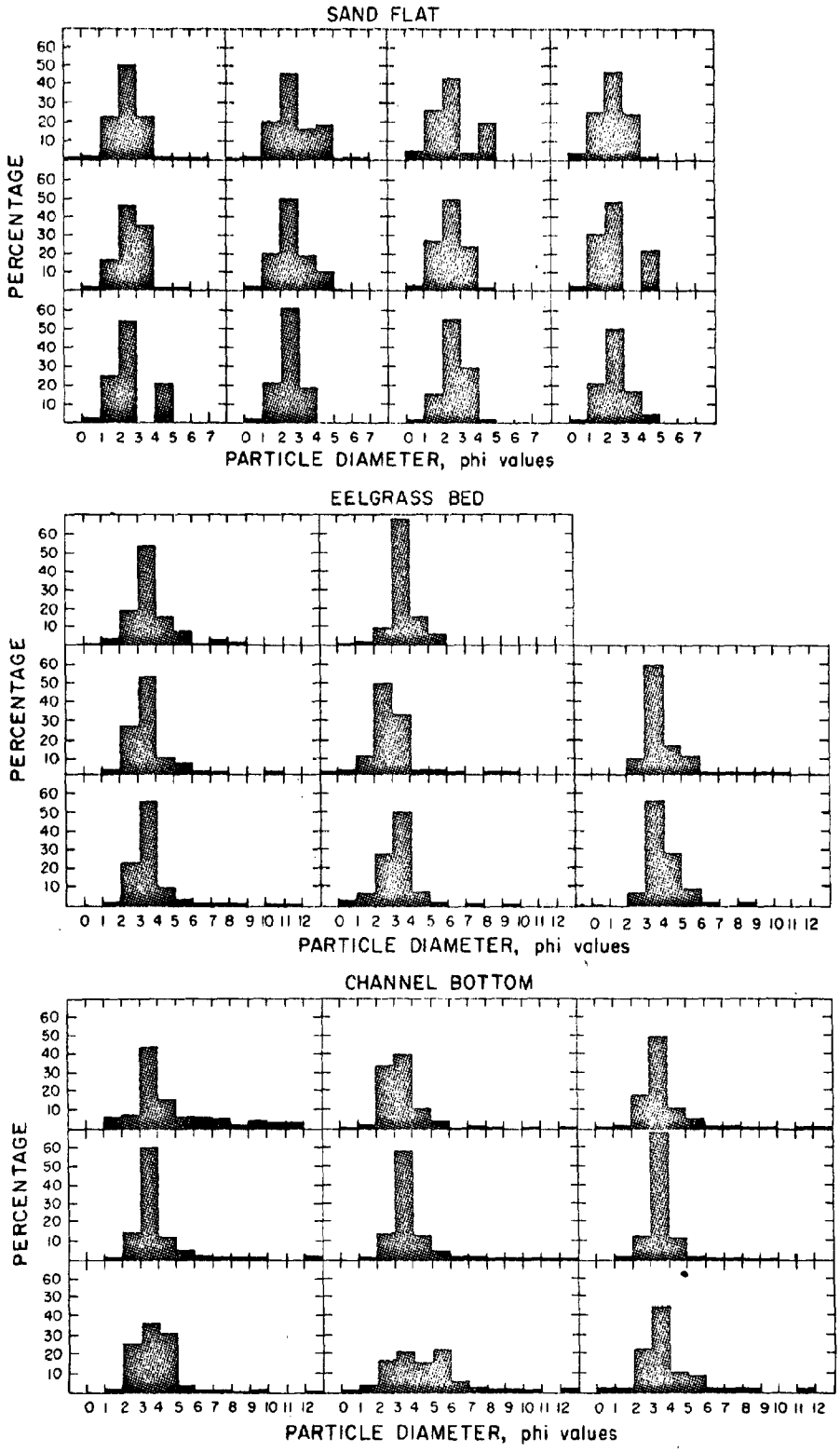


Fig. 7. Particle diameter distribution by weight in a sand flat, an eelgrass bed, and a channel bottom in an Alaskan lagoon. (After McRoy, 1966).

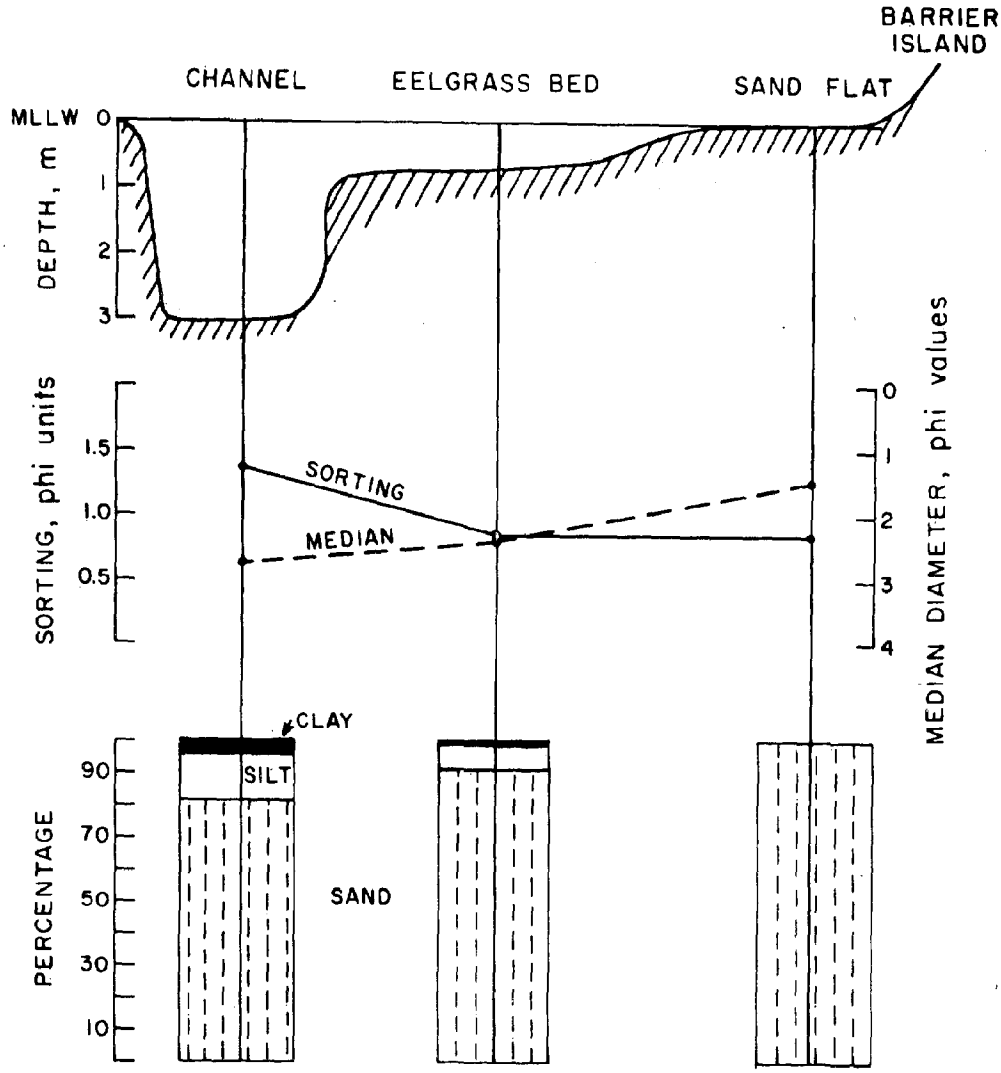


Fig. 8. Depth, sorting coefficient, median particle diameter, and sand, silt, and clay distribution from a sand flat, an eelgrass bed, and a channel bottom in an Alaskan lagoon. (After McRoy, 1966).

remarked that the presence of seagrasses indicated great bacterial activity and considerable variation in pH and redox potential. The latter favors the small photosynthetic organisms with a wide E_h range, i.e., blue-green algae, phytoflagellates, and diatoms. Zostera may cause the redox potential variation in the substrate. Wood (1953) discovered that Zostera released two reducing products which may produce ferrous sulfide directly and may result in reducing conditions that greatly accelerate sulfate reduction by Microspira (sulfur bacterium). ZoBell and Feltham (1942) believed that bacteria cause the reducing conditions in the substrate. Wood (1959a) found root hairs of Zostera in actual contact with particles of hydrated ferrous sulfide.

Much more research is necessary on the substrates supporting eelgrass. It appears that eelgrass conditions and is an integral interacting part of its substrate. Careless treatment of the marine soil may render it unfit for colonization by seagrasses.

pH

Cameron and Mounce (1922) stated that pH of water bathing eelgrass became more basic during daylight owing to photosynthesis and was almost always higher than that of immediately adjacent water. The pH lowered at night. On one series of readings Powers (1920) recorded a pH of 8.35 at 1035 hours in water over eelgrass. At 1345 hours the pH was 8.4. Broekhuysen (1935) found in a study of oxygen changes in water over eelgrass in Holland that pH was lowered as oxygen levels diminished at night. At Woods Hole Allee (1923b) reported that vertical gradients of pH existed in water over eelgrass at mid-afternoon. At substrate level pH was 7.3; at 24 inches off the bottom pH was 8.5; at 30 inches off the bottom (at water surface) pH was 9.0. Other readings gave the same vertical gradient relationships at low tide; with a moving tide the vertical gradients were wiped out. Allee (1923b) theorized that pH was more important than oxygen in explaining animal occurrence and behavior in eelgrass. In Washington Shelford and Towler (1925) found a diurnal range of pH of water bathing eelgrass from 8.8 to 7.7.

Waves, Surge, and Current

Tutin (1938) reported patchy growth of eelgrass on the south coast of England which was often exposed to fairly heavy seas.

Ostenfeld (1908) stated that a fairly sheltered locality is a prerequisite for successful eelgrass growth. Eelgrass would not grow along Danish open coasts where waves beat heavily.

It is known that severe water movement may erode seagrasses. Molinier and Picard (1952), working with two Mediterranean species, induced erosion in underwater meadows by placing stones on the bottom. Currents formed around the stones and eroded holes in the growth.

Moderate currents do not affect eelgrass growth. In fact, they seem to enhance it. I have seen some of the most luxuriant eelgrass in Puget Sound where currents periodically reach 3.5 knots, but have never seen persistence of plants where wave shock is regular.

Ecological data is summarized in Table 1.

SEASONAL PATTERN OF ACTIVITY

An eelgrass meadow is perennial. According to Setchell (1929) the individual leafy shoot or turion is biennial. It is formed as a lateral branch from the apical meristem of a turion terminal on a rhizome branch. The turion thus formed enlarges and from its own meristem forms four to six leaves (average of five). During the first year the meristem of the turion produces two lateral turions. In the second year the turion generates an erect flowering stalk which breaks off and is carried away after the flowering period.

Setchell (1929) listed these as the seasonal growth aspects: 1. Erect flowering stalk, ephemeral; 2. Terminal turions of the existing lateral branches developing into the erect flowering stalks in the succeeding season; 3. The lateral buds of the existing lateral branches developing into terminal turions in the succeeding year, these to develop into the erect flowering stalk of the second succeeding season.

The periodicity data listed here was garnered from Setchell (1929) for the wide-bladed form known as Zostera marina L. var. latifolia Morong in northern California. Seeds germinated in February. In March vegetative leaves were up to 14 cm. long. The lateral turions developed by July. In October the lateral turions had each developed lateral turions. This advanced state of development was probably a result of the lengthened growing season in California. Flowering stalks were formed in early spring.

In Puget Sound I found evidence for vegetative growth resumption (new roots and rhizome branches) after the winter cold rigor in February. New leaves were also in evidence. Summer leaves were wider and much longer than winter leaves. My records show that the winter period of reduced activity began in December. Flowering stalks appeared in May. In June seeds began germinating. Most germinating seeds were found in July. Standing crop data indicated a variability depending on tidal zone. Generally minimum biomass occurred in January and February. Maximum biomass was found during June through September. No heat rigor period existed in Puget Sound.

In Massachusetts Conover (1958) reported two periods of leaf decline and decay; one in June to early August and another in late September and October. Eelgrass began growth after winter dormancy in mid-spring and reached peak growth in summer. The largest standing crop developed between June and September with the maximum in July. The minimum plant biomass occurred in January and February. He associated the maxima and minima with maxima and minima in temperature and isolation. Conover reported heat and cold rigor periods for eelgrass in Massachusetts.

In Japan Arasaki (1950a) found that young turions developed throughout the year, except in mid-summer (July and August). Development reached a peak in winter and spring. Flowering stalks developed in late January with seeds developing in April and May. A summer decline set in in July and continued

TABLE 1

TABLE OF NUMERICAL CHARACTERISTICS OF HABITAT FACTORS

Habitat Factors	Plant Activity		
	Vegetative Growth	Flowering State	Seed Germination
Temperature			
Range	0 - 40.5°C.	----------	----------
Optimum	10 - 20°C.	15 - 20°C. (8-9°C. in Puget Sound)	5 - 10°C.*
Salinity			
Range	Freshwater - 42 o/oo	----------	----------
Optimum	10 - 30 o/oo	Same as optimum	4.5 - 9.1 o/oo
Depth-Light			
Range	1.8 meters above MLLW to 30 meters deep	----------	----------
Optimum	MLLW - 6.6 m. below MLLW (11 m. at high tide)	Effect unknown	No effect
Substrate			
Range	Pure firm sand to pure soft mud	----------	----------
Optimum	Mixed sand and mud	No effect	No effect
pH	7.3 - 9.0	Effect unknown	Effect unknown
Water Motion			
Range	Waves to stagnant water	----------	----------
Optimum	Little wave action. Gentle currents to 3.5 knots	Effect unknown	Effect unknown

* Arasaki (1950a) found no correlation with temperature. Most reports list best germination occurring in February and March. The temperature as listed may be incidental to a possible dormancy.

until late autumn, when growth activity resumed. It seems that no winter decline in activity was present in Japan. Seeds germinated in the field after a summer and autumn dormant period from late December to April. No dormancy was evident in germination tests in the laboratory. Thus, according to the temperature regime of Setchell (Fig. 4), in Japan there is a heat rigor period but no cold rigor period of inactivity.

It appears that periodicity of eelgrass activity is similar in Puget Sound and in Massachusetts. Puget Sound at 48°N. Lat. and Woods Hole, Massachusetts, at 41°N. Lat. would have slightly differing daylengths but perhaps not significant differences. In Puget Sound water temperatures become neither as low nor as high as recorded in Massachusetts, but a similar correlation can be made with changes in plant activity and rising or falling temperatures.

I suggest that owing to the much lower water temperatures in Puget Sound under which identical plant activities occur as compared with other geographical areas more research be concentrated on the interaction of plant growth and development and light.

In Denmark Ostenfeld (1908) reported that eelgrass produced four to six new leaves on each turion annually. Petersen (1913a) stated emphatically that Danish eelgrass turions each produced about 10 leaves in summer and about five more in winter. He further stated that standing stock of eelgrass reached a peak during July through September. In Holland Van Goor (1920) found that turions produced four to seven new leaves annually. I have found in Puget Sound that eelgrass produces a winter leaf crop and a different summer leaf crop, and that five leaves on the average are exposed at any one time. It is my calculation that the 15 leaves as calculated by Petersen (1913a) is close to the correct figure for Puget Sound eelgrass.

Seasonal data is summarized in Table 2 and Fig. 9.

PRINCIPAL INPUTS AND OUTPUTS OF ENERGY

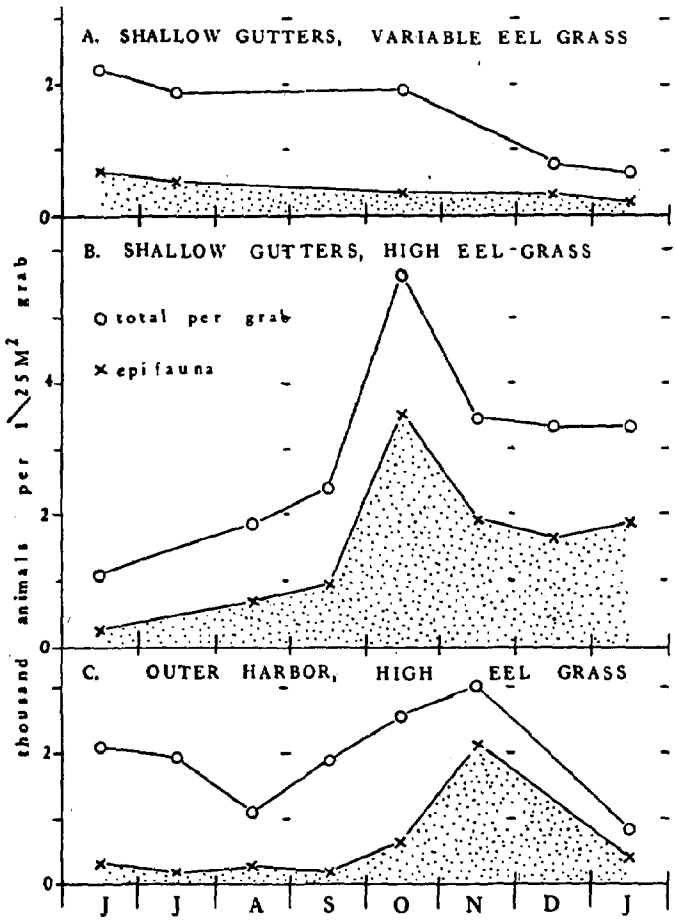
A host of reports concur in the importance of eelgrass as a source of nutrition. Petersen (1891) stated that the abundance of fish in Denmark was chiefly due to eelgrass. Petersen and Boysen-Jensen (1911) concluded that eelgrass was the main source of organic matter on the sea bottom in Denmark. These investigators also stated that organic detritus, derived chiefly from the decay of eelgrass, was the basic source of nutrition of animals in Danish marine waters, especially the benthic invertebrates. Dexter (1944b) concluded that detritus is probably the most important single item at the base of food chains in intertidal and shallow sublittoral communities. With the disappearance of eelgrass at Cape Ann, Massachusetts, a source of detritus was eliminated.

From a chemical study of the detritus of the bottom Boysen-Jensen (1914) decided that in more sheltered waters and fjords, the predominant source of organic matter was formed by eelgrass; in the more open waters, at least half the organic matter of the sea bottom was probably formed by eelgrass. He also concluded that animal communities of enclosed coastal waters were largely dependent on particulate organic detritus derived principally from decay of rooted vegetation in the *Zostera* belt.

TABLE 2

SEASONAL PERIODICITY OF EELGRASS

Country	Vegetative Growth				Flowering Stalk Produced	Seed Germination
	New Turions	New Leaf Production	Standing Stock	Root Growth		
United States						
Northern California (Setchell, 1929)	Probably June - October				Early Spring	February
Puget Sound, Washington	February (Production began)	February	Maximum- June - Sept Minimum- Jan - Feb	February	May	June - July
Massachusetts (Conover, 1958)		Mid-Spring (March)	Maximum- June - Sept Minimum- Jan - Feb			
Japan (Arasaki, 1950a)	Throughout year (except July - August)		Decline from July - late Autumn		Late Jan	Late Dec - April
Denmark (Petersen, 1913)			Maximum- July - Sept			



Seasonal changes in faunal abundance. Epifaunal trends are emphasized by the stippled pattern. The epifaunal increase in areas where the grass remains high corresponds to a decrease in areas where the grass defoliates.

Fig. 9. Seasonal changes in abundance of eelgrass epifauna (From Nagle 1968).

Blegvad (1914) found that a plankton net quickly filled with fresh plant fragments and particulate matter when pulled through water over eelgrass beds in Denmark. He stated that detritus formed the principal food of nearly all invertebrate animals of the sea bottom; next in order were the live benthic plants. He concluded that live phytoplankton was virtually valueless as nourishment for benthic invertebrates.

Darnell (1967a) stated that organic matter entering a system as detritus represents the total gross primary and secondary production of the community, less that contained in the protoplasm of producers, consumers, decomposers, and that oxidized through respiration. He concluded that the estuarine community was one of the most complex known, largely owing to the prevalence of organic detritus. Carriker (1967) wrote that rooted aquatics such as Zostera may be the chief producers of organic matter in sediments in shallow water. This organic matter serves as an energy source for a broad gradient of heterotrophic bacteria and larger benthic organisms, as a modifier of inorganic reactions through complex formation and chelation phenomena, and as a reaction system itself.

Petersen (1918) reported that benthic vegetation was not usually consumed in a living state but was spread after death in the form of detritus throughout the area. Ostenfeld (1908) recorded large masses of dead and decaying leaves from several places in Denmark. McRoy (1966) stated that large quantities of detached leaves were produced each year in Izembek Bay, Alaska. I can confirm this. Owing to mechanical breakage or biological degradation by bacteria and fungi, these leaves finally become detritus.

Table 3 lists quantitative data from a number of reports. I have followed the method of Petersen (1913a) to derive annual production of eelgrass matter. Petersen determined the maximum standing stock of eelgrass per square meter, doubled it, and used the latter figure for the annual production. This factor was derived from a calculated summer production of 10 leaves with one new rhizome node being produced for each new leaf. He ignored the five leaves probably produced in winter and later sloughed off. Thus, the data in Table 3 will be conservative. To get the amount of organic matter production, I have used the datum of Boysen-Jensen (1914) of 25% ash weight of eelgrass matter. This might also be conservative, as McRoy (1966) calculated the ash weight to be 20%. The nitrogen conversion factor is an average 2% of organic dry weight (Boysen-Jensen, 1914). The phosphorus conversion factor is 8% of the organic dry weight (McRoy, 1966).

My data for Puget Sound production derives from a study done from 1962-1964, including a complete field survey and later a transect study made monthly from two differing geographic areas in Puget Sound. Using the area-depth data from McLellan (1954) I have calculated that only 9% of Puget Sound actually supports eelgrass. Eelgrass grows over 131 square nautical miles; there is a total of 1514 square nautical miles in Puget Sound covered at mean lower low water. Thus, eelgrass grows over 4.5×10^8 square meters in Puget Sound.

McRoy (1966) determined that the mean caloric value of eelgrass leaves was 4125 cal./ash-free g.; the rhizome mean was 3967 cal./ash-free g. The overall mean was 4046 cal./ash-free g (Table 4).

TABLE 3

INPUTS AND OUTPUTS OF MATERIAL AND ENERGY CONTRIBUTED BY EELGRASS

Country	Production in Grams/Meter^2 Dry Weight Annual Growing Season: Matter	Production in Grams/Meter^2 Dry Weight Annual Growing Season: Organic Matter	Over Total Water Area	Total Annual Production Over Area (Dry Weight): Matter	Total Annual Production Over Area (Dry Weight): Organic Matter
Denmark					
Petersen (1913a)	1200	840	120 (organic matter)	8.2×10^9 kg. (8.2×10^6 metric tons)	6.2×10^9 kg. (6.2×10^6 metric tons)
Grøntved (1958)	277	208			
United States					
Alaska					
Izembek Bay, McRoy (1966)	372-648	279-486			150 metric tons
Massachusetts					
Great Pond, Conover (1958)	10-58	18-44			
California					
South Bay, Humboldt Bay. Keller (1963)	24-842	18-632			
Arcartia Bay, Humboldt Bay, Waddell (1964)	12-384	9-288			
Washington					
Puget Sound, Phillips (unpublished)	187-1078	143-809	17-97 (matter) (13-73 - organic matter)	8.4×10^7 - 4.85×10^8 kg. (8.4×10^4 - 4.85×10^5 metric tons)	6.4×10^7 - 3.6×10^8 kg. (6.4×10^4 - 3.6×10^5 metric tons)

TABLE 3 (Cont.)

INPUTS AND OUTPUTS OF MATERIAL AND ENERGY CONTRIBUTED BY EELGRASS

Country	Caloric Values - In KCal. (Organic Matter Dry Weight)			Nitrogen Released Organic Matter Dry Weight Metric Tons	Phosphorus Released Organic Matter Dry Weight Metric Tons
	Meter^2	Meter^2 Over Total Area	Total for Area		
Denmark					
Petersen (1913a)	3.4×10^3	486	2.51×10^{13}	1.24×10^5	4.96×10^5
Grøntved (1958)	842				
United States					
Alaska					
Izembek Bay, McRoy (1966)	1.13×10^3 - 2.0×10^3			3	12
Massachusetts					
Great Pond, Conover (1958)	73-176				
California					
South Bay, Humboldt Bay, Keller (1963)	$73 - 2.6 \times 10^3$				
Arcartia Bay, Humboldt Bay, Waddell (1964)	$36 - 1.2 \times 10^3$				
Washington					
Puget Sound, Phillips (unpublished)	579 - 3.3×10^3	69-392	2.59×10^{11} - 1.34×10^{12}	1.28×10^3 - 7.2×10^3	5.12×10^3 - 2.88×10^4

Table 4. Caloric and ash contents of eelgrass leaves and rhizomes in an Alaskan lagoon, 1964 (After McRoy, 1966).

Bed	Date	Calories (ash-free grams) Leaves		Rhizomes	Ash (%)
III	6 July	4268			16
		4326			17
VI	6 July	4163			17
				4811	32
				3320	20
				3776	24
				3962	19
III	7 Sept	3744			13
Mean		4125		3967	20
Standard deviation		131		312	
Grand mean			4046		
Standard deviation			160		

Fig. 10 represents gross productivity and respiration of eelgrass leaves taken by McRoy (1966) in an Alaskan lagoon. Fig. 11 presents data on chlorophyll a concentration of eelgrass in an Alaskan lagoon McRoy (1966).

Boysen-Jensen (1914) calculated by using pancreatin that in Danish waters there were 5 g. digestible proteids per square meter on the bottom. The bottom detritus was composed of up to 1% of pentosans (composition of the cell wall), found to be digestible by a number of animals. Both sources of food were found to derive from eelgrass.

Table 5 compares some sample net productivity data taken from Odum (1959) with yield data from my measurements of eelgrass from Puget Sound, Washington. Yield is calculated by substracting minimum from maximum standing stock. It is considered to be a minimum estimate of net production.

Table 6 compares net productivity of eelgrass from several geographic areas.

Conover (personal communications) related that 16 eelgrass plants produced 80 mg. carbon per day under experimental conditions for 14 days.

McRoy (1966) found that productivity of eelgrass was influenced by two levels of light intensity; one level was below 18 cal./cm.^{2}/hr., the other level was above 20 cal./cm.^{2}/hr. with no further correlation up to light saturation (Fig. 12). Burkholder and Doheny (1968) demonstrated increasing photosynthesis up to 60% of full daylight in New York. Above that level it decreased Table 7). Fig. 13 represents standing crop measurements of eelgrass from Alaska and Table 8 from Denmark.

Fig.14 represents the quantitative relationship of the eelgrass community of the Kattegat region of Denmark as calculated by Petersen (1918) and adapted by Milne and Milne (1951). Standing crop relationships were based on a series of reports of eelgrass and animal standing crops, and the calculation by Petersen (1918) that at each level of food pyramid there was a reduction in standing crop to 10% of the previous level. He concluded that the level lowest in the pyramid must have the greatest standing crop and that the herbivore level had less, etc. He also theorized that food fish in Denmark were far from economical to produce, inasmuch as they were all carnivores.

PRINCIPAL FOOD CHAINS

A great volume of literature deals with organisms directly or indirectly associated with eelgrass. I shall report on a few of the more significant papers. Further treatment of some data will be made in the section on disturbances.

Shelford et al. (1935) reported that all community constituents react on the habitat, but wherever it grows, eelgrass is the most important. In 1890 Petersen stated that the abundance of fish in Denmark was due chiefly to eelgrass. In a series of exhaustive reports from the Danish Biological Station (Ostenfeld, 1908; Petersen and Boysen-Jensen, 1911; Blegvad, 1914, 1916; Petersen, 1915, 1918) the fundamental role of eelgrass as the support of the food fish pyramid in Denmark was established (Fig. 6).

Boysen-Jensen (1914) demonstrated that in Danish shallow waters eelgrass was the principal source of organic detritus. Sverdrup et al. (1942) stated that bottom organic detritus is sometimes considered the main source of nourishment for most benthic invertebrates. Blegvad (1914) concluded that

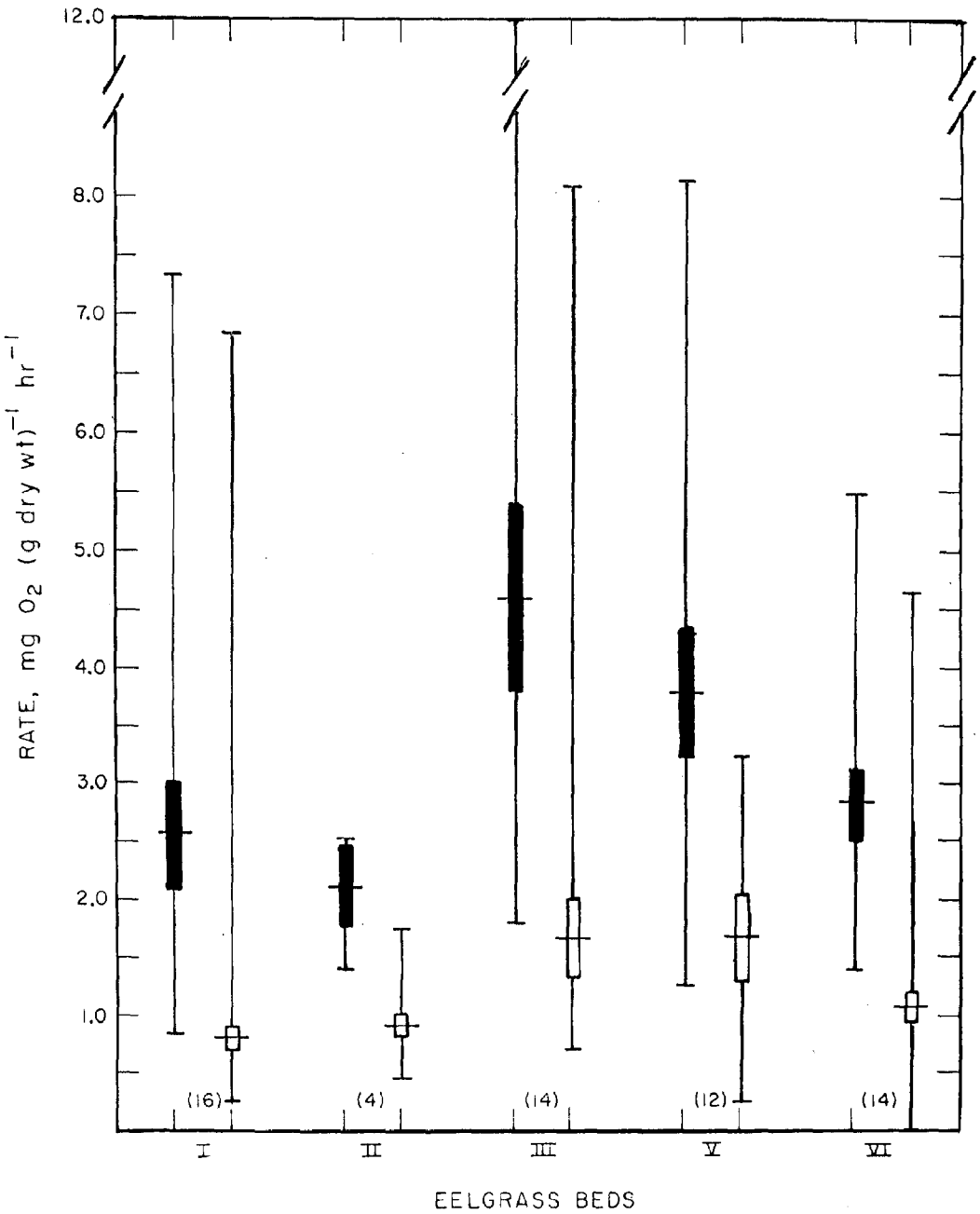


Fig. 10. Gross productivity (solid) and rate of respiration (open) of leaves from five eelgrass beds in an Alaskan lagoon. Number of observations mean, range, and one standard error about the mean. (After McRoy, 1966).

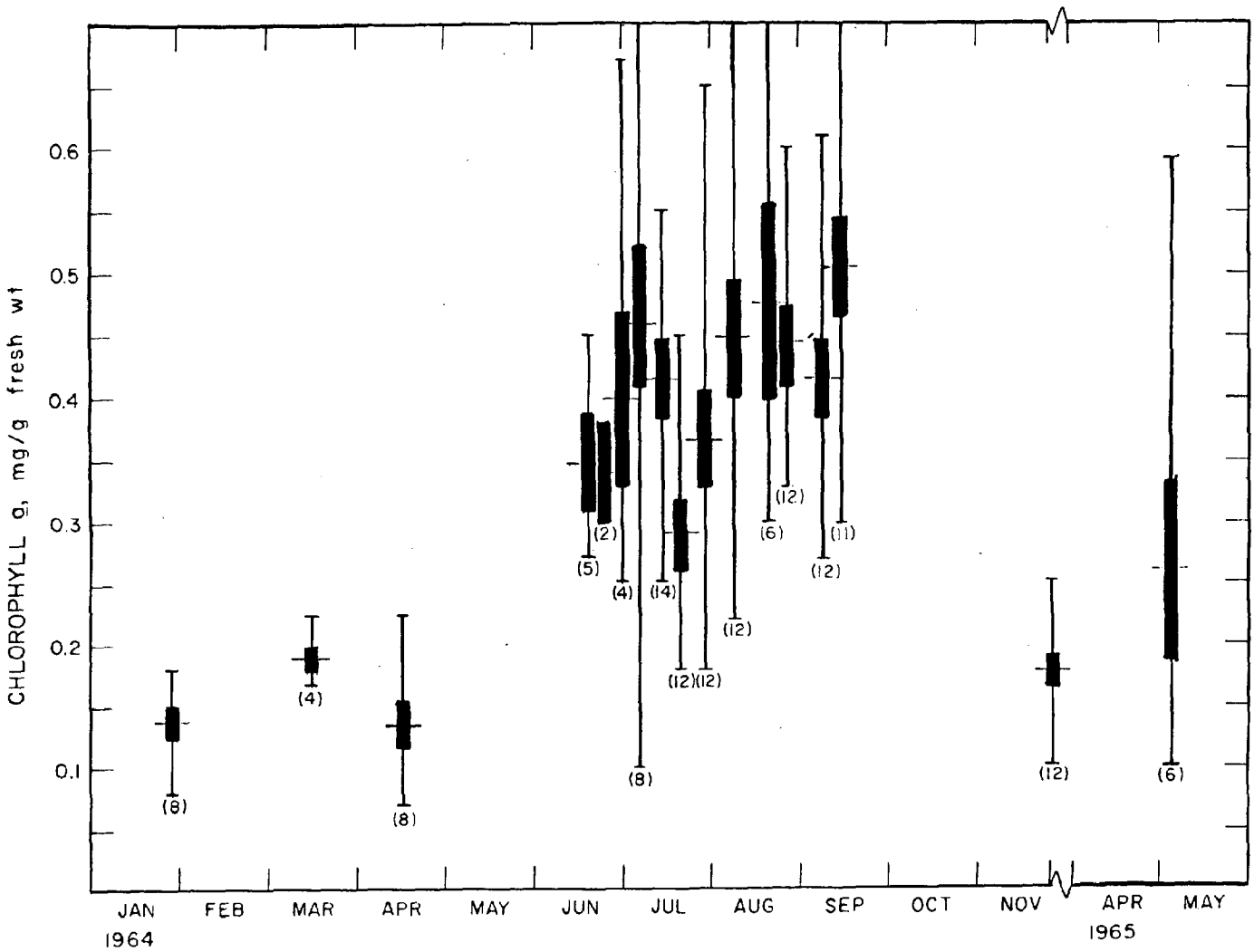


Fig. 11. Chlorophyll a concentration in eelgrass leaves from an Alaskan lagoon. Number of observations, mean, range, and one standard error about the mean. (After McRoy, 1966).

TABLE 5

COMPARISON OF NET PRODUCTIVITY OF CULTIVATED CROPS AND TWO MARINE SYSTEMS *

Crop	Grams/Meter^2 (Dry Matter)	
	Per Year	Per Day
Wheat, world average	344	0.94
Oats, world average	359	0.98
Corn, world average	412	1.13
Rice, world average	497	1.36
Hay, U. S. average	420	1.15
Sugar cane, world average	1725	4.73
Tall grass prairies, Oklahoma and Nebraska	446	1.22
Short grass prairies, Wyoming	69	0.19
Seaweed beds, Nova Scotia	358	0.98
Eelgrass (*Zostera marina*), Puget Sound, Washington	581	1.59
Denmark (Grøntved, 1958)	277	0.83

* All data except for eelgrass taken from data reported by Odum (1959). Eelgrass data is mine (unpublished data).

TABLE 6

COMPARATIVE NET PRODUCTIVITY DATA OF EELGRASS*

(Dry Weight of Tissue)

Country	Mg. O_2/g./hr.	Grams Carbon/m^2/growing season day (15 hr.)	Grams Carbon/m^2/Day
Denmark			
Petersen (1913a)[1]			0.6 - 2.5
Grøntved (1958)[2]			0.3
United States			
Alaska			
Izembek Bay McRoy (1966)[3]	2.05	2.0	
Washington			
Puget Sound Phillips[4]		1.55	0.6

[1] Calculated from standing stock by McRoy (1966).

[2] Calculated from yield data by McRoy (1966).

[3] Calculated from light-dark bottle experiments.

[4] Calculated from standing stock.

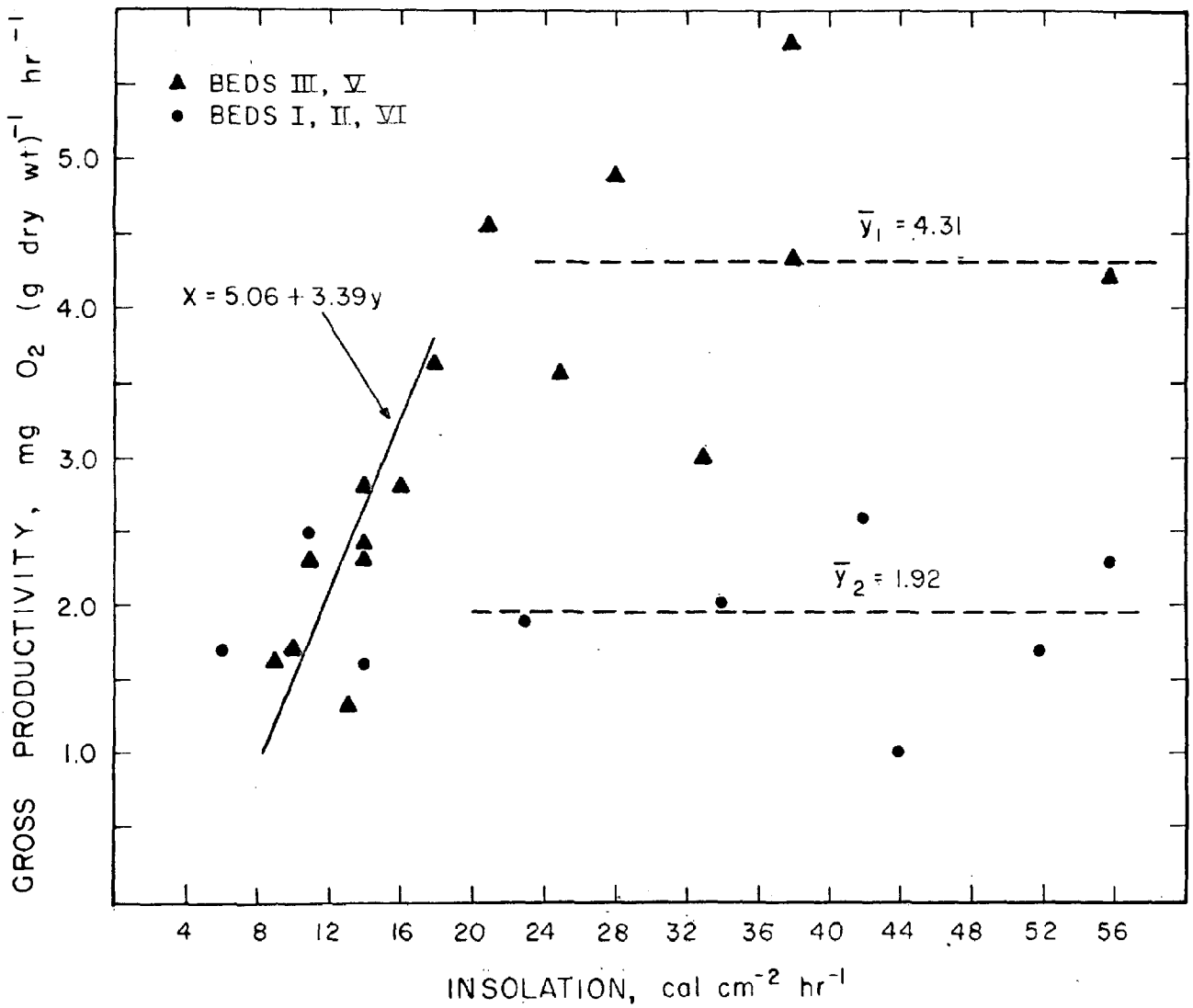


Fig. 12. Gross productivity of eelgrass as a function of insolation. Taken in an Alaskan lagoon. Means of duplicate observations. (After McRoy, 1966).

Table 7. Photosynthesis in different intensities of daylight shown by eelgrass and by epiphytic micro-algae associated with the eelgrass. Relative carbon fixation during a period of incubation with $Na_2{}^{14}CO_3$ is indicated by the number of disintegrations counted in a beta-counter. Note the increased counts with increasing light, except at the highest intensity of full sunlight. (After Burkholder and Doheny, 1968).

Per cent of daylight	1.6	10	20	60	100
Eelgrass	17,669	54,778	127,645	131,061	128,004
Micro-algae	443	3,261	6,041	5,748	5,177

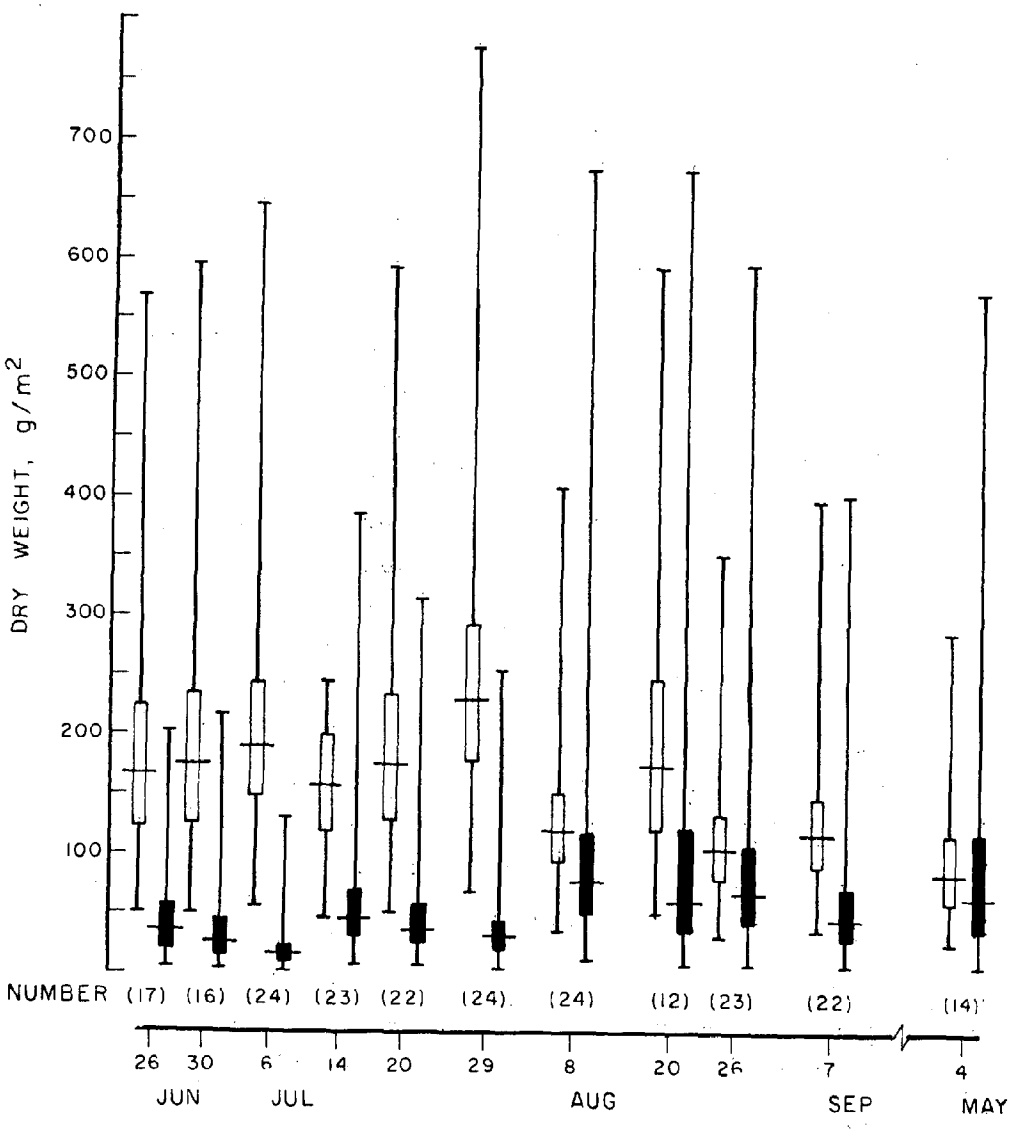


Fig. 13. Standing stock of eelgrass leaves (open) and rhizomes (solid) of beds on 11 dates, June 1964 to May 1965. Taken in an Alaskan lagoon. Numbers of observations, geometric mean, and 90% confidence limits about the mean and about an individual observation. (After McRoy 1966).

TABLE 8

PLANT LEAF ABUNDANCE IN GRAMS PER SQUARE METER TAKEN IN DENMARK (AFTER PETERSEN, 1913).

1911	Nyborg Fjord Hvidegrunden			Ø. f. Vresen		Svendborg Sund		Øresund udfor København
Dato:	6/4	7/8	12/8	8/4	12/8	14/9	14/9	19/8
Bundart:	Sand	Sand	Sand	Sand	Sand	Sort, frisk Bund	Sort, frisk Bund	Sand
Dybde i Meter:	4–7	4–5	5–7	5–7	5–7	2	2	4–5
Grøn Zostera	380	1856	1910	500	700	3700	3475	500
Rodder og usorterligt	1480	3494	1800	1700	1880	4800	3625	1700
Furcellaria	150	148	100	320	392	...	...	10
Fucus vesiculosus	190	24	...	65	96	...	...	104
Rødalger	75	116	160	50	256	...	...	272
Ascophyllum?	33	1,8	...	...	...	...	...	...
Laminariestykker	16	..	...	...	...	460	...	...
Chorda filum	...	...	...	...	...	...	...	50
Antal Prøver à 0,1 m²	50	25	25	50	25	10	Udført med Rive	25

1912	Limfjorden									
	Nykøbing Bugt							Skælholmen	Ø. for Faarøft Plantage	
Dato:	24/4	20/8	21/8	1/9	8/9	2/9	6/9	28/4	28/4	28/4
Bundart:	Sort Mudd. og Sand	Sort Mudder	Mudder	Mudder og Sand	Sort Mudder	Mudder	Sort Mudder	Sand	Sand	Sand og Detritus
Dybde i Meter:	1½–3-4	3	3	1–2	2–3	1	1	2–2½	2–2½	2½–3
Grøn Zostera	500	6979	5481	4600	3725	5225	3275	425	250	300
Rodder og usorterligt	800	5720	2808	3720	2750	3400	4175	1700	800	1500
Furcellaria	10	417	46	182	500	50	35	50	5	2
Fucus vesiculosus	...	...	...	52	...	50	...	...	...	...
Rødalger	...	...	...	...	...	...	...	...	60	...
Ascophyllum?	...	...	...	...	...	...	...	...	...	...
Laminariestykker	...	...	...	...	...	...	...	...	...	...
Chorda filum	...	...	...	...	...	...	...	...	...	...
Antal Prøver à 0,1 m².	50	12	13	25	10	10	Udført med Rive	50	50	50

1912	Nyborg Fjord					Limfjorden		
	Hvidegrunden			Udfor Sølyst		Nykøbing Bugt		
Dato:	10/4	10/7	19/9	13/7	19/9	27/8	30/9	31/7
Bundart:	Sand	Sand	Sand	Mudder	Mudder	Mudder	Mudder	Mudder
Dybde i Meter:	c. 6–8	c. 6–8	c. 6–8	3–4	3–4	3	3	3
Grøn Zostera:								
Hovedskud	}	700	1280	1460	1230	1500	950	3100
Sideskud	} 293	150	220	225	200	270	170	560
Blomstrende Skud	}	...	50	100	..	280	120	330
Løse, grønne Blade	} 127	325	950	1175	1060	450	410	2800
Tilsammen	420	1175	2500	2960	2490	2500	1650	6780
Rodder og usorterligt	1553	1880	4320	4600	1300	6300	4000	2400
Antal Prøver à 0,1 m².	30	10	10	10	10	10	10	10

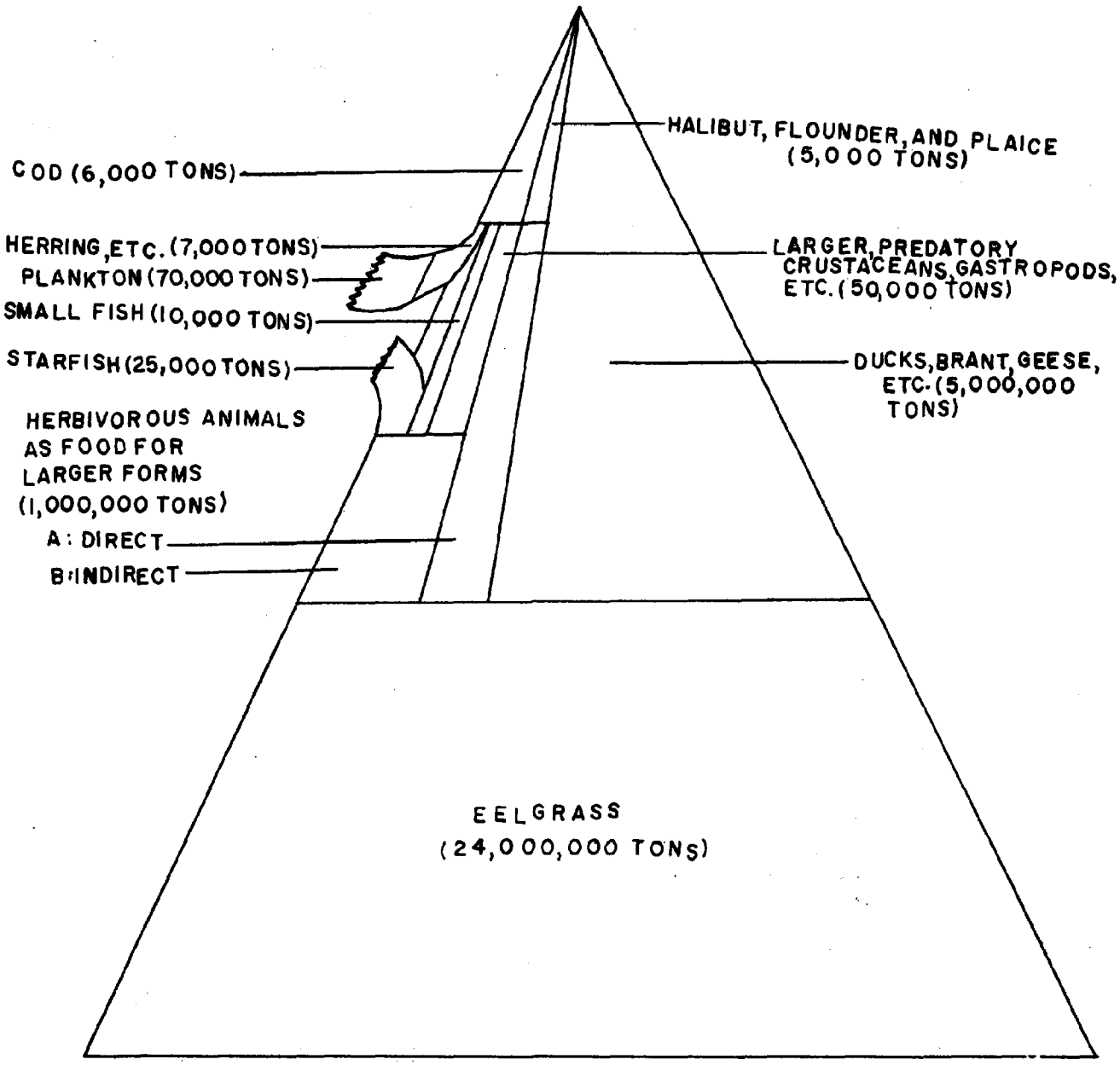


Fig. 14. Quantitative relationships of the eelgrass system in Denmark. The data used is from Petersen (1918). Diagram adapted by Milne and Milne (1951).

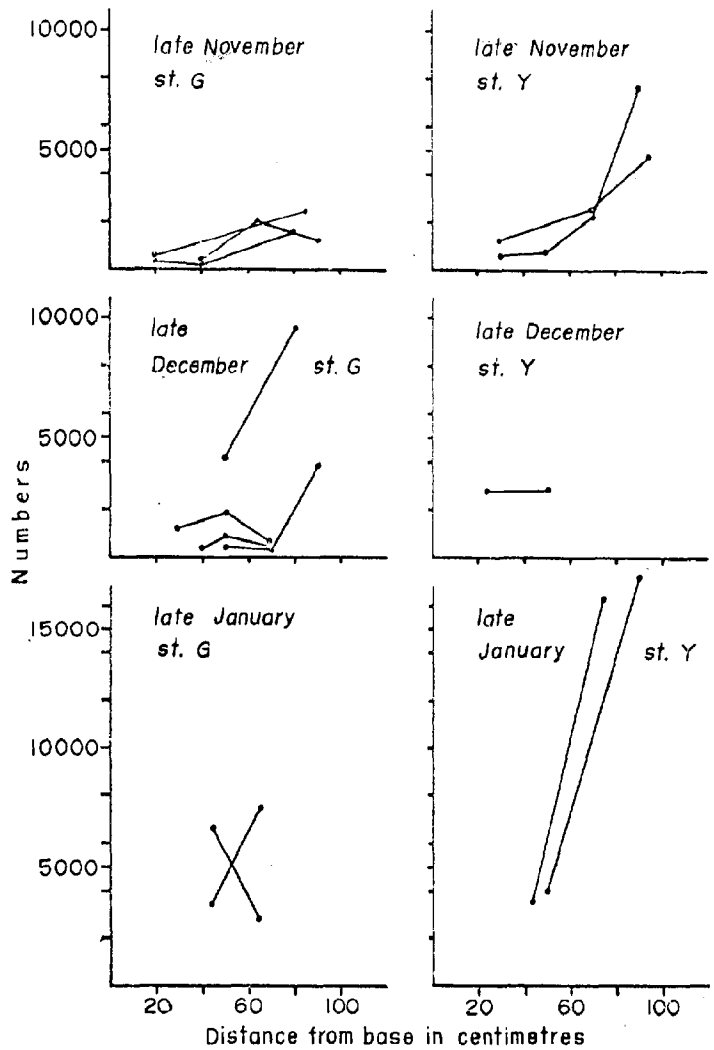
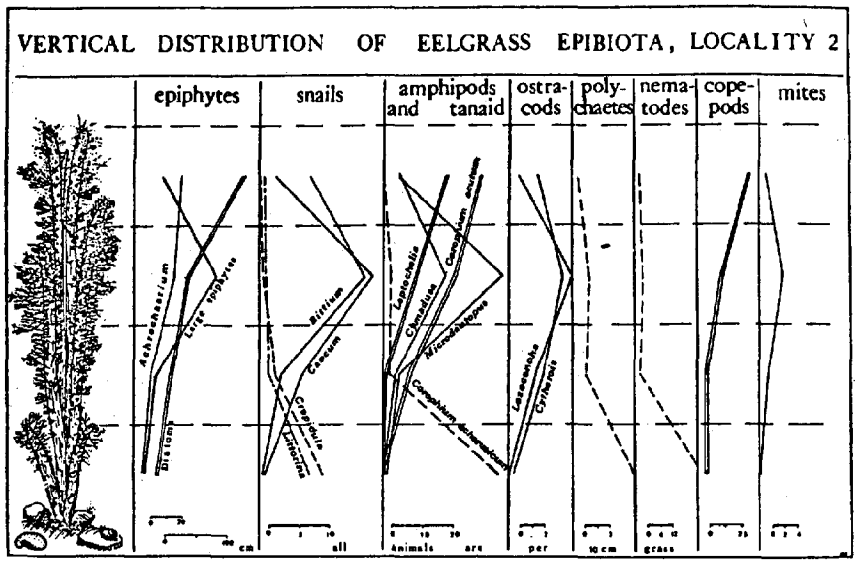
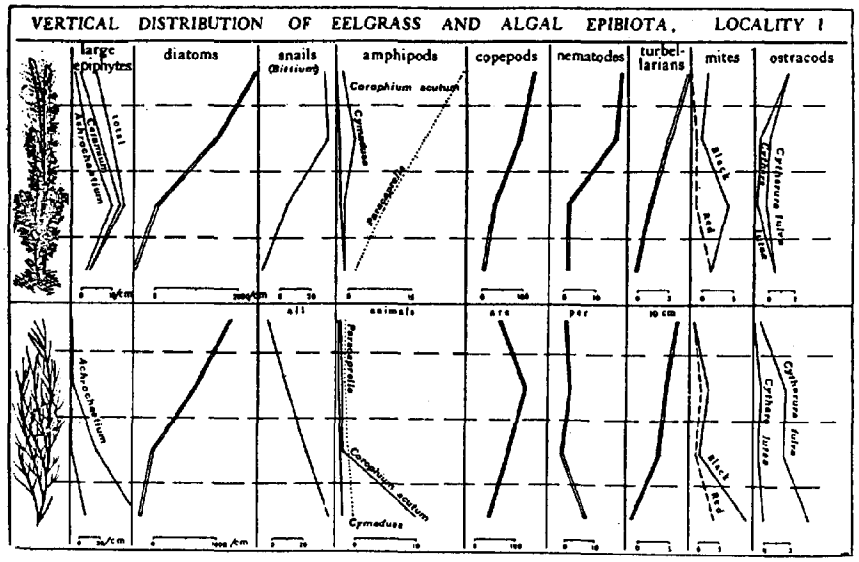


Fig. 15. The distribution of diatoms on the Zostera blades. Numbers per 1 cm.^{2} of the surface area. (After Kita and Harada, 1962).



Vertical distribution of eelgrass epibiota, locality 2, lagoon behind Tobey's Island, near Monument Beach, Mass. Dotted lines indicate animals which generally increase in abundance away from the bottom, dashed lines indicate animals which decrease in abundance away from the bottom, solid lines indicate variation with epiphytes, with single-ruled lines signifying variance with large epiphytes, double-ruled lines signifying variance with diatoms.



Vertical distribution of eelgrass and algal epibiota, locality 1, MBL pump dock, Woods Hole, Mass. Ruling of lines is the same as for Fig. 2. Notice that some patterns on the branched algae appear to be anomalous; this is related to the abundance of fine branchlets on the algae because other aspects of distribution are the same as for grass and less-branched algae.

Fig. 16. Vertical distribution of eelgrass epibiota in two localities in Massachusetts. (From Nagle 1965).

of 90 or more species of invertebrates investigated in Denmark, 69 (the most common) were some form of detritus eaters, while five were herbivorous and carnivorous, and 16 were carnivorous. MacGinitie (1935) found that almost all animals (95% by weight) associated with eelgrass in a California slough were detritus feeders.

Allee (1923a, 1923b) reported on exhaustive collections of invertebrates from Woods Hole, Massachusetts. He found 138 species associated with eelgrass beds. Stauffer (1937) organized the microhabitats of these animals into four categories: 1. Growing on the plants, 2. Swimming among plants, 3. Living on the mud surface, and 4. Burrowing forms.

In category one, most animals existed as epiphytes or clung to the leaves. These included anemones, encrusting bryozoa, hydroids, isopods, protoza (ciliates and flagellates) and small crabs. Certain animals attach to leaves for only a certain phase of their life history: herring lay eggs on the leaves (McHugh, 1967) which attract large numbers of gulls and other birds at low tides; the scallop (Pecten irradians) attached in the larval stage for about one month (Davenport, 1903). The leaves also form a substrate for bacteria (Zenkevitch, 1963; Carriker, 1967) and epiphytic plants. The bacteria are grazed by molluscs and cladocerans which are in turn used as food by fish.

Davis (1911) listed 42 species of plants known to occur on eelgrass in the Woods Hole, Massachusetts, area. Muenscher (1915, 1916) and Setchell and Gardner (1903) listed epiphytes on eelgrass from the west coast of North America. Wood (1959b) recorded a long list of epiphytic algal species on Zostera leaves, on each other, or on animals in Zostera beds in Australia. His list of diatoms on the mud surface in the Zostera was particularly long. He also stated that these plants were of great importance in the food chain of the Australian estuary and were most abundant in the seagrass community. The list also included an analysis of the fish which ate these diatoms.

Kita and Harada (1962) in Japan and Nagle (1965) in Massachusetts diagrammed the abundance and distribution of epibiota on leaves (Figs. 15 , 16).

Phifer (1929) found mats of diatoms in an eelgrass bed in the Puget Sound area, Washington. Portions of the mat floated to the surface during the day. I have also observed these mats of diatoms in eelgrass in this region. Based on Wood's observations in Australia, these mats are probably important in the eelgrass food chain.

In category two, are the fishes and crustaceans such as the amphipods, copepods, and cladocerans. Blegvad (1916) stated that the eelgrass plant belt in Denmark was the richest in fauna in their fjords. The water over the plants teemed with small crustaceans, molluscs, and small fish, which then were fed on by many food fish. Outside this plant belt the fauna was much poorer.

A great number of organisms lived on the mud surface in and near the eelgrass system, responding to the rain of organic matter. These included the entire list of detritus feeders, i.e., crabs, many different molluscs, worms, some fish, small and larger commercial shrimps, amphipods, rotifers, myriads of nematodes, cucumbers, brittle-stars, starfish, sea urchins, and occasionally sea-pens. Many flatfish live on the substrate surface in eelgrass. Sverdrup et al. (1942) and Zobell and Feltham (1942) reported on

the importance of bacteria in the substrate as food for marine invertebrates. The latter authors found an average of 1×10^7 living bacteria per cc. of mud. They felt that mud-dwelling animals derive a large amount of their nourishment directly from ingestion of bacteria. Burkholder and Doheny (1968) also counted numbers of bacteria in an eelgrass area in New York (Table 9). Zobell and Feltham (1938) found that certain marine invertebrates could live almost indefinitely on an exclusive diet of bacteria. Thus, the substrate of the eelgrass system is a very rich habitat.

Among burrowing forms are worms, some molluscs, a few brittle stars, a cucumber, and some crustaceans such as the blue mud shrimp or mud prawn (Upogebia). Carriker (1967) stated that root hairs are used as food by the mandibulate burrowers. MacGinitie (1935), working in a California estuary, sifted the top inch of soil from a 45 inch circle. He recovered 947 individual animals from 34 species.

Very few organisms utilize the fresh plants as food. This was first stated by Ostenfeld (1908) and later by Petersen (1918). This was also the conclusion of Day (1967), working on a species of Zostera in a South African estuary. Of those animals that do eat eelgrass are periwinkles, some crabs, certain fishes, perhaps isopods, and a number of water fowl. Wood (1959a) reported that in Australia swans denuded large areas of an estuary of Zostera, in their quest chiefly for rhizome material. A sizeable literature exists pertaining to the use of eelgrass by waterfowl in North America and Europe. Cottam (1934) established that eelgrass constituted 80% of the winter food of the sea brant goose and was an important food to several other species. McRoy (1966) estimated that Black brant and Canada geese consumed about 17% of the standing stock of eelgrass in Izembek Bay, Alaska, during the summer and autumn feeding period. Each bird was calculated to require about one m^2 of eelgrass per day.

My conclusion is that the eelgrass system is one of the richest in terms of variety and abundance of life in the sea. Eelgrass plays several roles: one is as a substrate for organisms which could not otherwise live on a soft substrate; secondly, it is used as food for a small number of animals; thirdly, products resulting from eelgrass breakdown support a large diversified community of animals; lastly, the physical presence of the plant on an unconsolidated muddy bottom provides protection and cover for organisms requiring quiet water or silt-free water. Thus, the association with eelgrass is direct and indirect. It appears that a very large number of animal forms have adapted in interrelated ways to the various types of microhabitats that an eelgrass system presents.

Fig.17 (MacGinitie, 1935) and Fig.18 (Blegvad, 1916) are diagrams of food chains in areas where eelgrass is either dominant or very abundant. Fig.19 is a food chain diagram from an estuary in South Africa which contained a species of Zostera (Day, 1967).

Odum (1962) found that two types of food chains were present in each ecosystem, i.e., the grazing chain made up of herbivores feeding on living plants and their predators and the detritus chain made up of herbivores which feed on dead plant material and their predators. Phillipson (1966) concluded from Odum's data that in the marine ecosystem the grazing chain was

Table 9. Bacteria in the eelgrass area of South Oyster Bay, July, 1966. Samples were taken with sterile bottles and estimates of the numbers were made by dilution plating on nutrient seawater agar. (After Burkholder and Doheny, 1968).

Location of Samples	Type of Sample	Bacteria per gram or ml
Station D	mud	1,300,000
	water	27,700
	eelgrass	68,964,000
East of Squaw Island	mud	200,000
	water	30,000
	young eelgrass	1,680,000
	old eelgrass	28,728,000

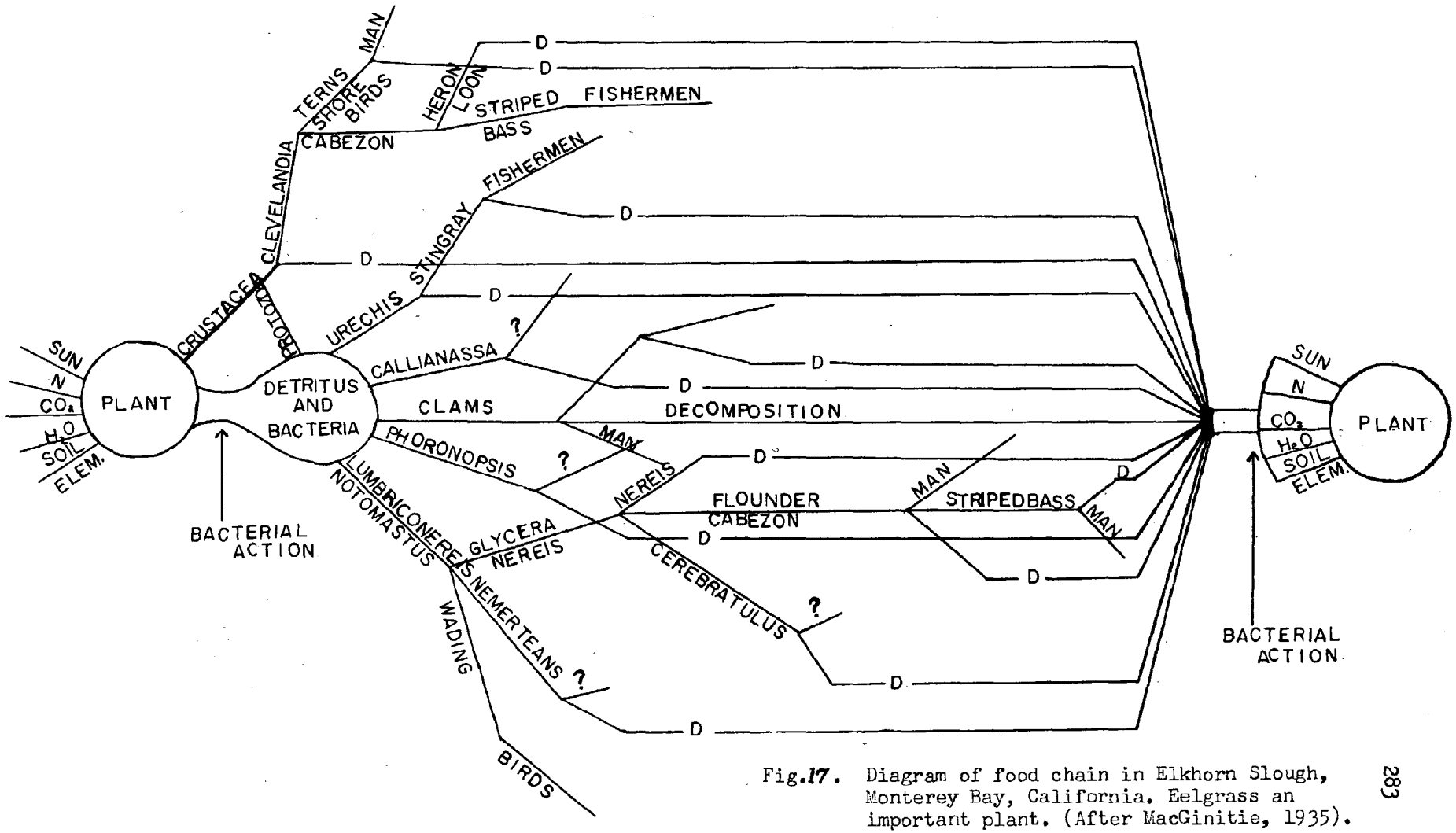


Fig.17. Diagram of food chain in Elkhorn Slough, Monterey Bay, California. Eelgrass an important plant. (After MacGinitie, 1935).

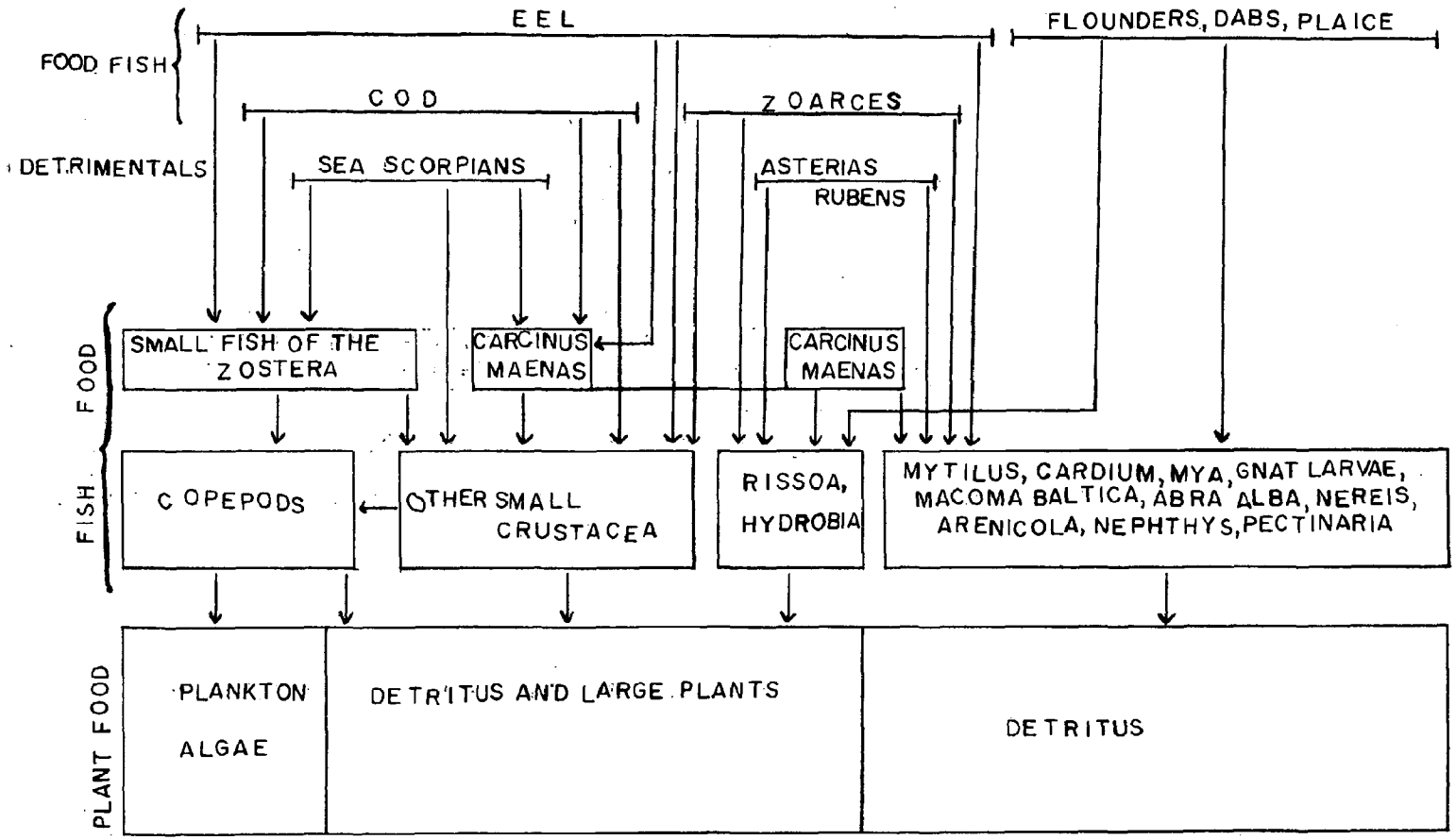


Fig. 18. Schematized food chain in Nyborg Fjord, Denmark where eelgrass is the dominant plant. (After Blegvad, 1916).

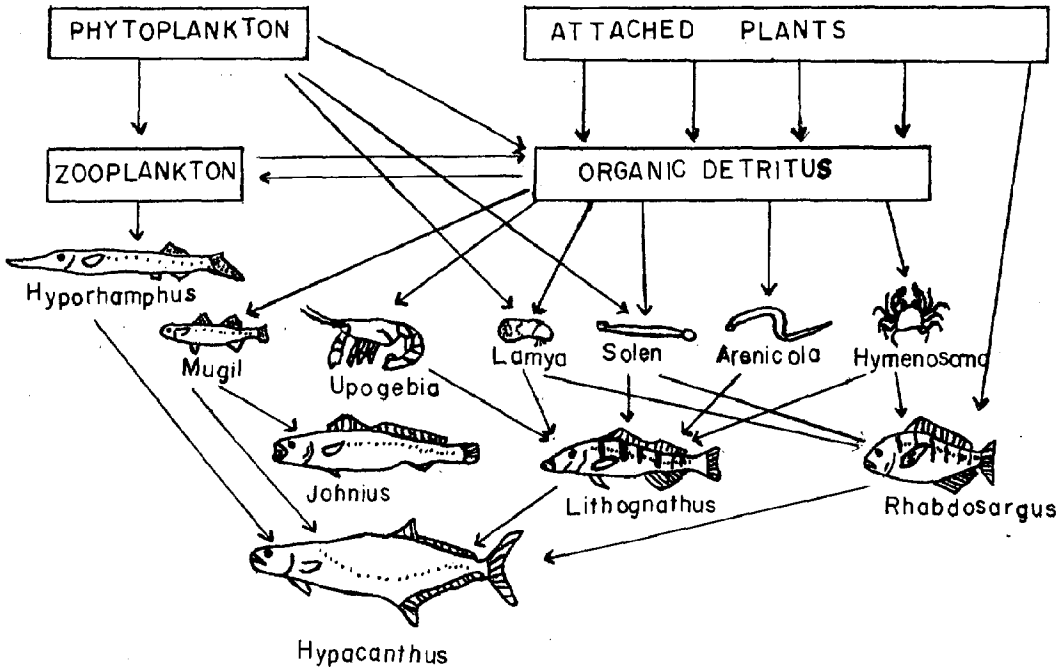


Fig. 19 Food chain in Knysna Estuary in South Africa where Zostera is abundant. (After Day, 1967).

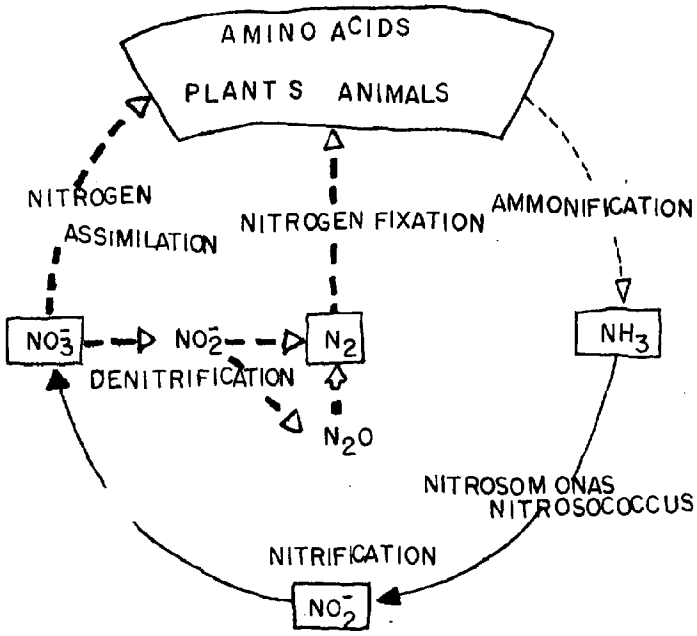


Fig.20. Typical nitrogen cycle (After Stanier et al., 1957). All stages depicted occur in the sea.

the major pathway of energy flow. From the literature reviewed for the eelgrass system, it is evident that the detritus food chain is overwhelmingly predominant.

CHARACTERISTIC MINERAL CYCLES

Three mineral cycles and a diurnal oxygen fluctuation are discussed. Several general texts in ecology give generalized cycles for sulfur, phosphorus, and nitrogen through an ecosystem. The specific application of research to these mineral cycles with regard to the eelgrass system is sparse. There is some work presently being done on the nitrogen cycle in an eelgrass bed (C. P. McRoy, personal communication). Burkholder and Doheny (1968) reported analyses of eelgrass leaves and rhizomes from New York (Tables 10, 11, 12).

Nitrogen

Eelgrass is known to contain a relatively large amount of nitrogen in its leaf cells. Boysen-Jensen (1914) determined that on the average the nitrogen content was 1.5% (leaf dry weight). This was compared with a content of 1.1% from hay from several species of grass. He also determined that the relative amount of nitrogen varied according to the age of the leaf, being highest in green young leaves, a lower level as the leaf aged, then rising again as the leaf turned black (decomposing state).

The nitrogen cycle consists of six stages: ammonification, nitrification, nitrogen assimilation, denitrification, nitrogen reduction, and nitrogen fixation (Sverdrup et al., 1942) Bacteria responsible for carrying out these phases have been described from the sea. Many have been found along coastal areas. The role of nitrogen assimilation is that of green plants, eelgrass in this instance. It is highly probable that uptake is by diffusion through epidermal leaf cells (my note). Gessner (1968) has found a network of perforations in the leaf cuticle of eelgrass which extend to the epidermal cell membranes. Before this function can be precisely defined in eelgrass, the plant part where nutrient uptake occurs must be located.

Denitrification occurs under anoxic conditions. In almost all substrates I have examined in eelgrass beds a black sulfide layer has been present, accompanied by the odor of sulfide. I assume this to be an evidence, not only of reducing conditions, but also of anaerobiosis.

Fig. 20 is a schematic diagram of a typical nitrogen cycle (Stanier et al., 1957).

Sulfur

Wood (1953, 1959a) noted that Zostera produced two organic reducing substances, one a sulfur compound, the other a nitrogen compound. He theorized that they may directly produce ferrous sulfide in mud and may bring about reducing conditions that greatly accelerate sulfate reduction by the bacterium Microspira. He reported seeing root hairs in actual contact with particles of hydrated ferrous sulfide.

Stages in the sulfur cycle are: sulfate reduction to hydrogen sulfide

Table 10. Proximate analyses of Zostera leaves, rhizomes and old shoots washed up on the beach. Analytic values are given as per cent of dry weight. (After Burkholder and Doheny, 1968).

Determination	Zostera Sample		
	leaves	rhizomes	beach grass
Total solids[1]	89.01	96.62	86.82
Moisture[2]	10.99	3.38	13.18
Fat (ether extract)[1]	2.29	0.91	1.04
Protein (N x 6.25)[1]	10.63	6.14	10.55
Ash[1]	8.80	32.62	15.68
Crude Fiber[1]	61.70	59.94	63.50
Carbohydrate (other than crude fiber)[2]	5.60	-	-
	- -	calories/100g	- - -
Caloric value[3]	85.5	32.8	51.6

[1]Official Methods of Analysis of the Association of Official Agricultural Chemists (1965).

[2]By difference

[3]Based on caloric equivalents per gram of 9, 4, and 4 for fat, carbohydrates, and protein, respectively.

Table 11. Mineral levels in Zostera leaves.[1] (After Burkholder and Doheny, 1968).

Mineral	Per cent in ash	Per cent in Zostera leaves[2]
Calcium	5.15	0.453
Magnesium	7.69	0.677
Phosphorus	4.39	0.386
Potassium	2.52	0.222
Zinc	0.031	0.0027
Iron	0.39	0.034
Manganese	0.49	0.043

[1]By atomic absorption spectroscopy

[2]Moisture-free basis

Table 12. B vitamins in *Zostera marina* leaves from South Oyster Bay, and *Ulva lactuca* from Middle Bay, August, 1967. Values are given in micrograms per gram of dry material. (After Burkholder and Doheny, 1968).

Species	Biotin	Thiamine	Niacin	Pantothenate	B_{12}
Zostera	.04	.38	11.13	16.34	.022
Ulva	.12	.94	11.80	1.20	.256

(by the anaerobic desulfovibrio bacterium) and on to ferrous sulfide; sulfate reduction by heterotrophs to hydrogen sulfide; oxidation of hydrogen sulfide by thiobacilli directly to sulfates or spontaneously to sulfur by oxygen, or by colorless, purple, or green bacteria in a series of steps to sulfates.

Baas Becking and Wood (1955) found the following groups of the sulfur cycle in the mud of the Zostera community in Australia: 1. Sulfate reducers; 2. Thiobacteria - three main groups: a. Thiooxidans, b. Anaerobic Thiobacillus denitrificans, and Th. thioparus; 3. Purple bacteria - Chromatium; 4. Green bacteria - a small green streptococcus. Wood (1959b) specifically added these forms to the list: Desulphovibrio (sulfate reducer), Chlorobium (a green bacterium), and large numbers of heterotrophs (including anaerobes).

Baas Becking and Wood (1955) found that certain marine algae as well as Zostera secrete reducing substances into the mud, and thus within a few hours lower the E_h (redox potential) to a value within the limits of sulfate reduction. They found that Zostera was a constant companion of the sulfate reducers.

Fig.21 is a schematic illustration of the sulfur cycle as presumed to occur in the eelgrass system (after Odum, 1963a).

Phosphorus

Conover (personal communication) remarked that eelgrass harbored a phosphorous pool in its cells. McRoy (1966) calculated that if the annual leaf drop for Izembek Bay, Alaska, were only 10% of the standing stock, it would contribute 150 metric tons of organic matter with 12 metric tons of phosphorus, four times the amount of nitrogen. I can find little literature specifically relating a phosphorus cycle to eelgrass.

Oxygen

Broekhuysen (1935) reported on oxygen changes over a 24 hour period in water over an eelgrass field in Holland. It represents the most thorough series of readings in the literature. He found that conditions in the eelgrass became anoxic for several hours at night (from 1 a.m. until 6 a.m.). He also found that at 3 p.m. there was a supersaturation of oxygen in the water (260%). He concluded the oxygen in an eelgrass field is subject to great variations in a short time. He also reasoned that animals in the vicinity of eelgrass must be adapted to the anoxic conditions and to the lowered pH levels attendant with the low oxygen.

Fig. 22 is a chart depicting the oxygen changes (after Broekhuysen, 1935).

McRoy (1966) discovered that eelgrass was capable of active fermentation. This ability would probably be important as an alternate pathway of energy supply for eelgrass in shallow water.

ECONOMIC VALUE OF EELGRASS SYSTEM

Petersen (1918) recorded the total yearly catch of Denmark's food fish but put no dollar values on them. Most of the food fish were associated

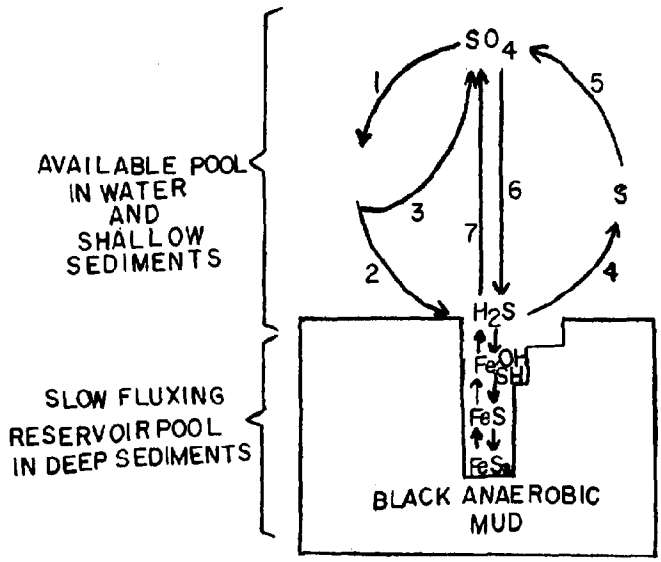


Fig.21. Sulfur cycle as applied to the eelgrass system. (After Odum, 1963a, Baas-Becking and Wood, 1955). 1. Primary production by autotrophs; 2. Decomposition by heterotrophic microorganisms; 3. Animal excretion; 4, 5. Steps by colorless, purple, and green sulfur bacteria; 6. Desulfovibrio bacteria (anaerobic sulfate reducers); 7. Thiobacilli bacteria (aerobic sulfide oxidizers).

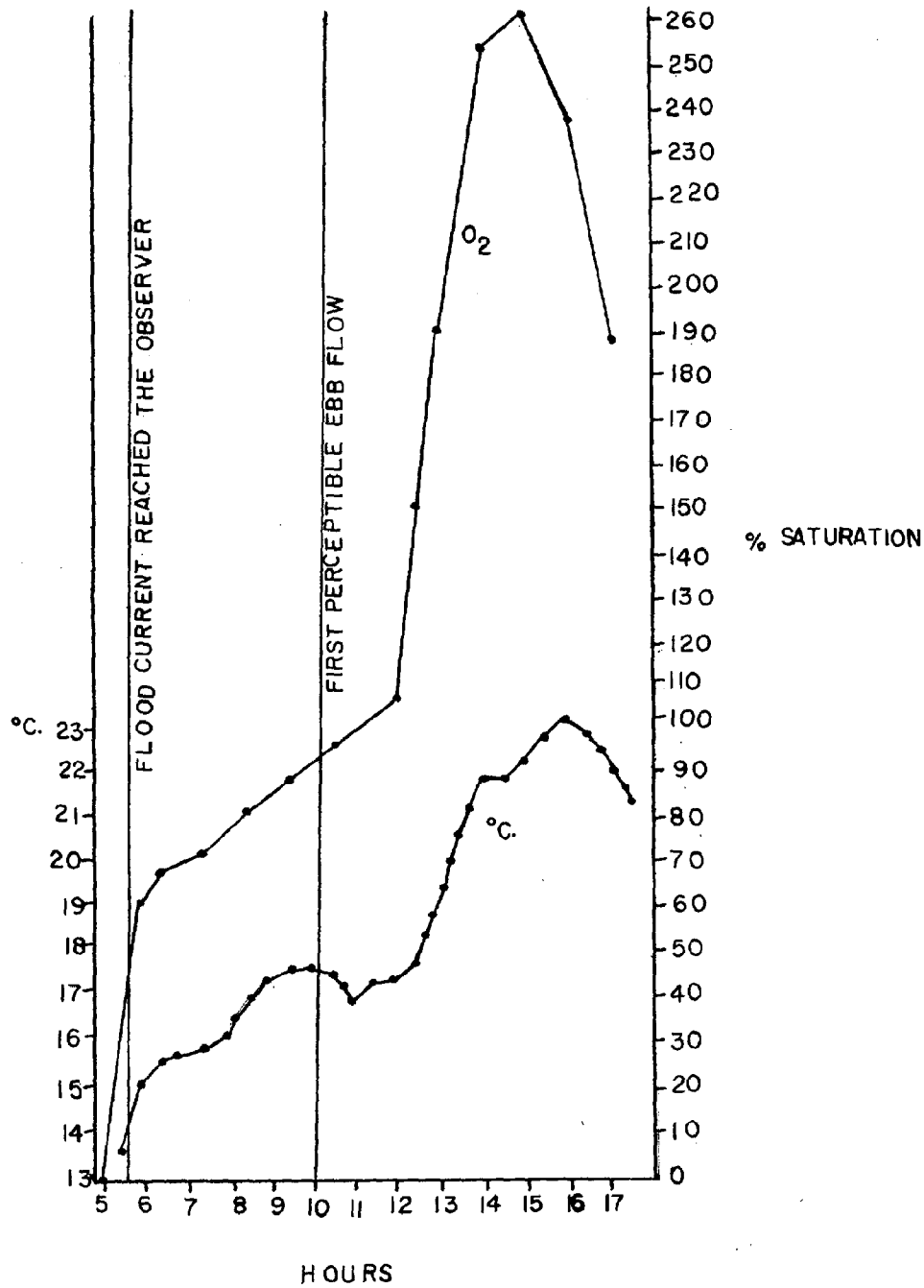


Fig. 22. Oxygen changes in an eelgrass field in Holland. (After Broekhuysen, 1935).

with the eelgrass pyramid.

Petersen (1918) stated that eelgrass fibers could be used in explosives of the gun cotton type. Cottam (1934) reported that ashes of eelgrass were found at ancient Danish village sites where it had been burned for salt and soda. He also stated that the plant was used for fuel on islands deficient in wood. Eelgrass leaves have been used for filling mattresses near coastal towns. Farmers along coasts have used leaves as bedding for domestic animals. Cottam (1934) added that in North America and Europe the dried fiber was used in packing, upholstering, and as compost in fertilizer. Eelgrass was used in the Netherlands in dike construction.

Cottam (1934) stated that the most extensive use of eelgrass was as insulation. Griffiths (1922) conducted tests on eelgrass and found it had a very low thermal conductivity with excellent keeping qualities. Leaves have much silica and iodine, many air cells, harbor no vermin, and will not burn or rot. It is excellent in insulation and as a sound deadener. Griffiths (1922) stated that a house built in 1635 at Dorchester, Massachusetts, used eelgrass as insulation in the walls, and that the eelgrass was still well preserved after two and one-half centuries. Lewis (1931) reported that at Isle Verte the price of eelgrass leaves had been at $40.00 per ton when the supply was at 3600 tons per year, but dropped to $20.00 per ton when the supply dropped to 600 tons in 1929. Collection was made at low tide with scythes. Cottam (1934) stated that two Boston firms in 1929 imported 1,725 tons of dried leaves from Nova Scotia. Great Britain, the Netherlands, and France also exported leaves. He stated that the Netherlands exported 2,000 - 3,000 tons annually. The United States produced 5,000 tons per year between 1913-1927, with a price at the factory of $20.00 - $30.00 per ton of dried leaves. In 1956 an article appeared in the Main Coast Fisherman concerning the use of eelgrass as insulation. Fisherman from Nova Scotia were again harvesting eelgrass leaves, pressing them into batts for home insulation and sound proofing. The price ranged from $21.00 - $30.00 per ton depending on shipping distance. One firm in Nova Scotia in 1955 produced about two million square feet of leaves.

The indirect value of eelgrass as the base of the pyramid for food fish, clams, scallops, oysters and waterfowl would be difficult for me to estimate. In addition eelgrass, owing to the long leaves and their density and the mat which the basal rhizomes form in the substrate, hinders substrate erosion. The dollar values of erosion prevention would also be difficult to estimate.

DISTURBANCES AND EFFECTS ON SYSTEM

Very little definitive work has been done on the effects of chemical pollution on eelgrass. Much has been written inferring these effects. Certainly such pollution would lower light penetration in the water, perhaps both quantitatively and qualitatively. It would appear that a relatively high BOD in the water would not seriously affect the ability of eelgrass to conduct respiration since it can conduct active anaerobic respiration (McRoy, 1966).

Two reports have mentioned pollution effects, one by mechanical disturbance, the other a possible effect of oil spillage. Stevenson and Emery (1958) reported that eelgrass, once a common and widespread colonist in Newport Bay, California, was reduced to isolated patches following disturbance of the bottom by dredging. They attributed the disappearance of eelgrass to deposition of substrate material eroded and carried by the water following dredging.

Duncan (1933) stated that eelgrass stocks were reduced over wide areas in England, and that crude oil spillage from shipping was probably responsible. Cotton (1933) refuted that damage was done by oil. By contrast Diaz-Piferrer (1962) found that Thalassia (a tropical seagrass) was severely damaged by oil spillage in Puerto Rico, and that effects on plants were residual and long-lasting.

The best documented case of massive disturbance of a natural system is that of eelgrass. In 1931 eelgrass along all coasts of the Atlantic Ocean of North America and Europe began to die and disappear. Tutin (1942) stated that by 1933 - 1934 90% of the plants had been destroyed. Moffitt and Cottam (1941) reported that along most areas of the Atlantic coast of the United States 99% of standing stocks of eelgrass were destroyed in a year. Some areas experienced total loss of eelgrass.

The disease was termed "wasting disease". Renn (1936) reported that healthy green leaves became discolored, spotted, and brown streaked. This led to tissue deterioration and loss of leaves. Ultimately rhizomes decayed.

Cottam (1934) concluded that the speed and destruction of eelgrass initiated in 1931 represented an epidemic unknown in scope elsewhere in botanical history. Bacteria, fungi, and a mycetozoan, Labyrinthula, were all found in diseased plants, and the latter in healthy plants. Thus, it has been popular for most recent authors to attribute wasting disease to Labyrinthula. Porter (1967), after an exhaustive cytological study of the genus, concluded that Labyrinthula was a saprophyte and penetrated eelgrass leaves only when the latter became moribund. Tutin (1938) correlated periods of eelgrass reduction with excessively cloudy years. The cause of the massive disturbance still remains unknown.

Moffitt and Cottam (1941) reviewed the eelgrass condition on the Pacific coast of North America. They found that standing stocks fluctuated from year to year, with some decline occurring from 1937 - 1941 along much of the coast. As far as I am aware, neither the Pacific coast of North America nor that of Japan have suffered the epidemic.

Many papers enumerate the loss of marine life following eelgrass disappearance. Most of the work concentrated on the animals used as food, but the loss of forms intermediate in the pyramid was extensive.

Waterfowl dependent on eelgrass for food declined sharply. In the Netherlands Bruijns and Tanis (1955) reported a two-thirds reduction of the Brant goose in some parts. Ranwell and Downing (1959) reported that at Scott Head Island in Great Britain the Brant goose declined from a population of

250,000 to 22,000 after eelgrass declined in 1931. In the United States sea brant, Canada geese, and black ducks suffered considerably when eelgrass declined (sea brant numbers fell 80% by 1934; Moffitt and Cottam, 1941). They also found that Black brant geese on the Pacific coast declined when eelgrass declined.

Soft-shelled and razor clams, lobsters, and mud crabs declined severely when eelgrass disappeared (Dexter, 1944b) Milne and Milne (1951) reported that cod, flounder, shellfish, scallops, crabs, and other food animals were reduced when eelgrass disappeared. Marshall (1947) found that, whereas scallop populations fell sharply in some areas, numbers soared in the absence of eelgrass in the Niantic River in Connecticut.

The best documented case history of the consequences of the eelgrass system disturbance is that of Allee (1923b) and Stauffer (1937) from Woods Hole, Massachusetts. Allee listed 138 species of animals found in or among eelgrass, of which Stauffer considered 55 to be characteristic of the eelgrass system. Stauffer found that animals formerly reported as occurring on the plants or swimming among the plants were gone. Only animals formerly reported from the mud surface or burrowing in the mud remained. Only 36 characteristic species remained, a reduction of one-third. No new species were found since 1923. The burrowing animals were the most conspicious group (Table 13).

Amai et al. (1951) reported that decaying Zostera in Japan supported heterotrophic bacteria and colorless flagellates. One flagellate was the food of the larval oyster, Ostrea gigas. The development of this organism coincided with the spawning of the oyster. The decay of eelgrass leaves is a natural annual event in late summer.

Dexter (1950) found that with the return of a small stand of eelgrass by 1949 in Goose Cove at Cape Ann, Massachusetts, the whole complex of animal life normally associated with eelgrass returned. The complex did not return in nearby areas where the eelgrass did not return.

Prenant (1934) studied the effects of eelgrass decline in the Morbihan, a bay on the southern coast of Brittany in France. The fauna changed as currents scoured the sediments, and epiphytes decreased in number when the plants disappeared.

Mechanical effects of eelgrass disappearance were noted. Wilson (1949) stated that in Salcombe Harbor in Great Britain sand banks were lowered by two feet or more after eelgrass disappearance. He also stated that buried fauna in Salcombe Harbor and flat fish in the Isles of Scilly declined or disappeared. Eelgrass not only stabilizes the bottom but also reduces water turbidity by retarding current flow through the plants. Decline of eelgrass thus results in substrate erosion, the smothering by silt of molluscan and other filter feeders, and the loss of the base of the food pyramid for a host of food animals in the sea.

Allee (1934) in a schematic diagram of community evolution in the Woods Hole region, placed the eelgrass community in a line of succession beginning in deeper water, leading to sand bars, to muddy sand communities, then to muck

TABLE 13

SHOWING THE RELATIVE ABUNDANCE OF CHARACTERISTIC SPECIES IN THE N. W. GUTTER LAGOON BEFORE AND AFTER THE DISAPPEARANCE OF THE EELGRASS[3]. (AFTER STAUFFER, 1937).

I. Animals formerly growing on the plants	Occurrence	
	Before	After
Coelenterata:		
Sagartia luciae	*[4]	
Bryozoa:		
Bugula turrita	***	
Arthropoda:		
Idothea baltica	*	
Mollusca:		
Bittium alternatum	**	—
Lacuna vincta	**	
Littorina sp.	***	**
Mitrella lunata	*	
Total number of characteristic epiphytic species	7	1
II. Animals formerly swimming among the plants		
Annelida:		
Podarke obscura	*	
Arthropoda:		
Crago septemspinosus	*	*
Gammarus sp.	**	**
Palaemonetes vulgaris	**	**
Virbius zostericola	**	
Mollusca:		
Pecten irradians	**	
Total number of characteristic swimming species	6	3
III. Animals living on the surface of the mud		
Coelenterata:		
Hydractinia echinata[5]	**	**
Arthropoda:		
Carcinides maenas	**	
Libinia dubia	*	
Libinia emarginata	*	*
Pagurus longicarpus	***	***
Pagurus pollicaris	*	*
Neopanope texana sayi	**	**
Limulus polyphemus	**	*
Mollusca:		
Crepidula convexa	**	**
Crepidula fornicata	*	*
Crepidula plana	**	*

III. Mud-surface forms (continued)	Occurrence	
	Before	After
Nassa obsoleta	***	**
Nassa trivittata	**	**
Modiolus demissus	***	
Mytilus edulis	**	
Ostraea virginica	*	*
Total number of characteristic mud surface species	16	12
IV. Burrowing forms		
Nemertea:		
Cerebratulus lacteus	*	*
Micrura leidyi	***	
Echinodermata:		
Leptosynapta inhaerens	***	*
Thyone briareus	***	**
Annelida:		
Amphitrite ornata	**	*
Arabella opalina	**	**
Cistenides gouldi	**	**
Clymenella torquata	**	***
Diopatra cuprea	*	
Glycera sp.	***	*
Lumbrinereis tenuis	*	***
Maldane urceolata	*	*
Nereis virens	***	
Scoloplos fragilis	***	***
Spio setosa	*	***
Phascolosoma gouldi	*	*
Arthropoda:		
Pinnixia chaetopterana	*	*
Mollusca:		
Cumingia tellinoides	**	
Ensis directus	*	*
Mactra lateralis	*	*
Mya arenaria	***	*
Solemya velum	**	
Tellina tenera	**	**
Venus mercenaria	**	**
Chordata:		
Dolichoglossus kowalevskyi	*	*
Total number of characteristic burrowing species	25	20
Grand total of characteristic species	55	36

[3] Allee ('23a) lists 138 species found in the eel grass areas from 1915 to 1921. Of these, 18 species were never found in the N. W. Gutter and 64 species were so rarely present there as to be found only during one or two years, or else were so scarce in number as to be found by only one or two collecting parties a year; these very rare species have been considered unimportant in the population as a whole and have therefore been omitted from this list for the sake of clarity.

[4] * Occasional: Before—found in less than 33 per cent of Allee's collections. After—forming less than 2 per cent of the 1936 population.

** Common: Before—in 33 per cent to 50 per cent of Allee's collections. After—forming 2 per cent to 5 per cent of total population.

*** Abundant: Before—in over 50 per cent of Allee's collections. After—forming 5 per cent or more of the total population.

[5] Since the hermit crabs, on whose shells this hydroid lives, are to be found on the surface of the mud, this seems the best place to classify Hydractinia.

and salt marsh communities, and finally to land communities.(Fig. 23). The role of eelgrass in promoting sedimentation is well established.

Dexter (1944) stated that since the loss of eelgrass in Massachusetts danger to swimmers by drowning through entanglement in the leaves was removed.

INTERACTION OF EELGRASS SYSTEM WITH DEVELOPING CIVILIZATION

Cottam (1934) suggested the introduction of other seagrasses after the wasting disease decimated eelgrass stocks in 1931. It has been my experience with Florida tropical seagrasses and Puget Sound eelgrass that transplanting may effect establishment of plants, but spread by vegetative means is exceedingly slow.

Dredging in shallow marine bays for creation of real estate is common. All too often these bays support large stocks of seagrasses. In addition to the erosion and silting problems created (Stevenson and Emery, 1958), chemical equilibrium in the substrate is disrupted. In Australia Wood (1959a) found that after denudation of Zostera by swans, the substrate became oxidized and thus unfit for future growth of the plant.

Keller and Harris (1966) stated that trends were developing in the use of tidal basins for channels, oyster culture, reclamation for industrial development and agriculture, and sewage outlets which reduced the acreage of eelgrass beds and initiated disturbance conditions of growth of remaining beds. In certain instances the effect of eelgrass in promoting sedimentation is detrimental to human industry. However, any dredging in an eelgrass bed may have consequences beyond the immediate site of activity. Molinier and Picard (1952) found that the simple placement of stones in an established growth of Mediterranean seagrasses induced erosion in the plant beds by setting up erosive currents around the stones. Once started this erosion continued.

I suggest that biologists and representatives from the industry and governmental agencies set priorities on the use of areas supporting the eelgrass system. More research is needed before anyone could state that industrial activity in shallow water is inimical to survival of the eelgrass system in the area of involvement. However, at the present time it appears that activities of the type conducted by industries situated on the marine coast could be harmful to the system. Certainly dredging and possibly the outlet of untreated sewage, oil, and other industrial wastes are harmful to eelgrass. With the use of water for cooling of industrial machinery, care will have to be exercised on behalf of eelgrass. In the event marine water is ever involved, water that is too warm could disrupt eelgrass periodicity.

Some effort has been made to control eelgrass in areas of oyster culture. In the Maritime Provinces of Canada where eelgrass is moderately dense, oyster collecting is difficult. Taylor (1954), Thomas (1967), and Thomas and Duffy (1968) investigated mechanical and chemical means of eelgrass removal in oyster

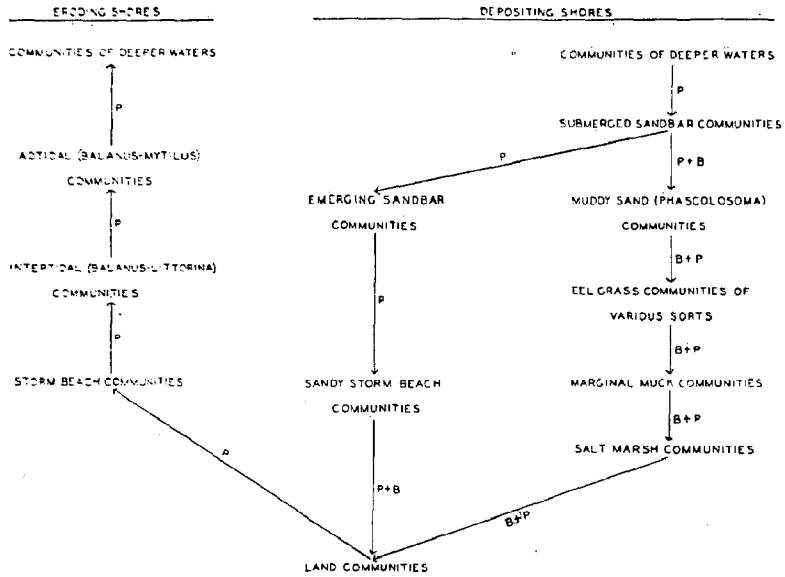


Fig. 23. Schematic diagram of community evolution in the Woods Hole region. Arrows show direction of succession. Letters show the principal forces acting; P, physiographic; B, biotic. (After Allee, 1934).

culture areas. It appears that siltation in an eelgrass bed is detrimental to good oyster growth and development.

Polikarpov (1966) reported concentration factors of a variety of radioisotopes in eelgrass in relation to other marine plants and animals. Of the isotopes tested, eelgrass ranked with the lowest values of the marine plants tested. Three exceptions existed: eelgrass had high concentration factors for zirconium, germanium, and niobium. Eelgrass had the lowest concentration factor for iodine of any marine plant tested.

Attempts have been made to replace eelgrass lost through the wasting disease or to introduce it into new areas. Addy (1947a,b) conducted studies on propagation of eelgrass from vegetative plants and by seeds. In both forms he obtained successful colonization when done under proper conditions and time of the year. Mr. Robert D. Jones (personal communications) and I have attempted transplanting of vegetative eelgrass. Mr. Jones' work was done in Alaska; mine was done in Puget Sound, Washington. In both cases transplants were successful in establishment. In my experiment the vegetative transplants initiated flowers and seeds. I found that horizontal spread of plants over the substrate was slow by vegetative means. If an extensive area is to be colonized in a short time, I suggest that either an extensive number of transplants be made or recolonization should be made by seed propagation.

RESEARCH NEEDS AND GAPS IN OUR KNOWLEDGE

McRoy (1966) gave a good review of work needed on eelgrass.

The perfection of culture techniques demands priority. Until we can hold and manipulate plants in culture, little definitive work on its ecological life history can be done.

More productivity measurements are needed from plants from different tidal levels, different latitudes, different seasons, under different light intensities, and under different water temperatures. In the laboratory light and temperature effects should receive concentrated effort. Studies should include not only their respective or interacting effects on growth and development, but also their effects on rates of respiration and photosynthesis.

Plant breeding needs to be done to develop strains of eelgrass resistant to the types of disease which decimated Atlantic Ocean stocks in 1931.

In the field a variety of studies should be made. Substrate dynamics are important. The factors controlling the redox potential should receive careful attention. Studies on nutrient cycles are beginning, but more needs to be done. Qualitative and quantitative food web studies are needed.

McRoy (1966) suggested further chlorophyll a studies on a seasonal basis. Caloric estimates are needed from seasonal samples of sexual and vegetative plant parts.

A study of the detritus contributed by eelgrass is needed, as to amount,

type, chemical content, caloric values, and the effect on the physical structure of the habitat.

Lastly, when the laboratory and field studies have been made and correlated, it should be possible to effectively establish eelgrass by transplanting it as reclamation of disturbed lands or into newly created eelgrass ponds.

Chapter C-7B

SHALLOW SALT PONDS

Very shallow marine waters with good tide, wind, and wave circulation develop ecosystems in which bottom vegetation is a major photosynthetic producer such as the eelgrass, turtle grass, and algal bottoms. Many small marine estuaries of pond size not regularly flushed out by the rivers belong in this category. Because they have definite boundaries provided by the shores, they form more discrete ecosystems than some in which boundaries must be drawn by the student. The boundaries form the tidal currents so as to produce internal gyrals and channels that organize the biological communities, different species being adapted to local spots according to current, access to passing food, and associated sedimentation (Fig. 1-4). The deeper ponds may have plankton processes exceeding bottom metabolism. The salt pond is particularly common on glacial coasts where ponds formed as kettles. Many ecosystem studies have been done in shallow ponds of New England. Figs. 1-8 for example, show ponds on Martha's Vineyard and Nantucket islands of Massachusetts. Some are lake size.

EXAMPLES

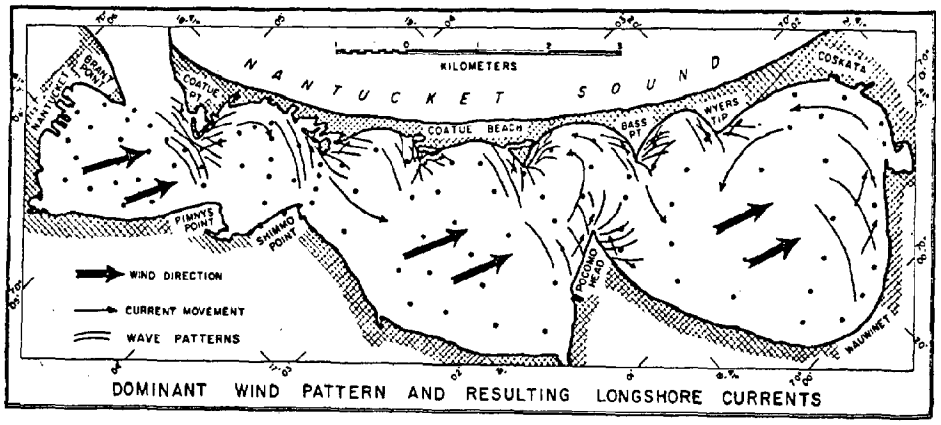
Shown in Figs. 3, 5, 6, and 7 are data from Great Pond, Plymouth, Massachusetts. The prominent bottom plants were studied by John Conover (1958). They had a distribution related to the current and a seasonal pulse with the light (Fig. 7). There was temporal substitution of species dominance in the course of the year (Fig. 6).

Shown in Figs 8-10 are data on Oyster Pond showing an appreciable plankton production as well as bottom photosynthesis. High productivity is shown in the curves of oxygen and pH (Fig. 8) with a corresponding accumulation of dissolved carbohydrates. Growth in the soft shell clam, Mya, was related in part to flagellates (Figs 9 and 10).

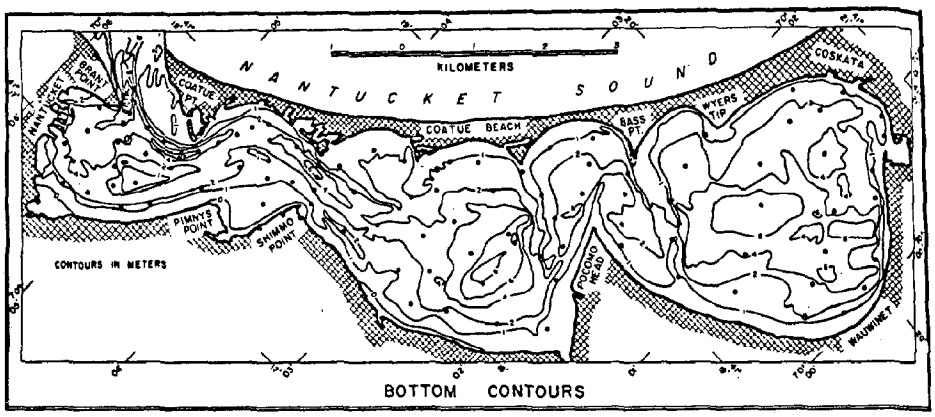
An example of small fish populations in a pond which serves as a nursery is given in Fig. 11, showing the net movement of larval pipefishes in from the sea.

An example in which there is a 7 to 21% river contribution to food energies is given by Barlow, Lorenzen and Myren (1963) in Fig. 12 and Tables 1-3 on Forge River.

Southward in the subtropics where tides are mainly less, the shallow salt pond may develop hypersaline characteristics at its periphery as described by Nichols (See Chapter A-6).

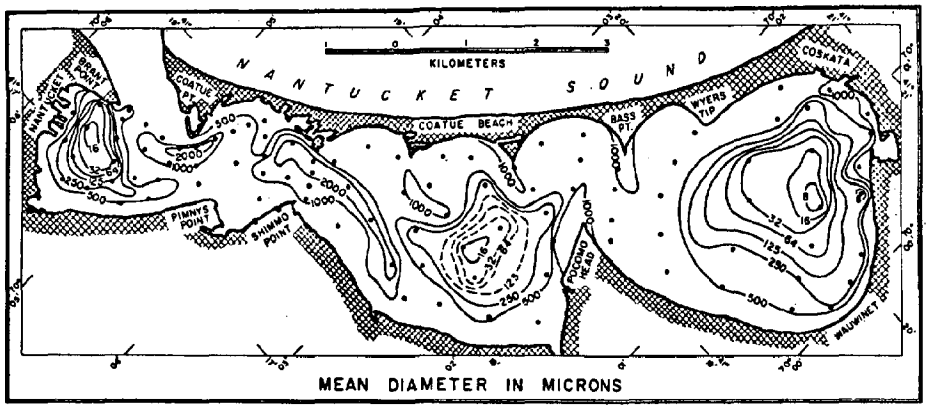


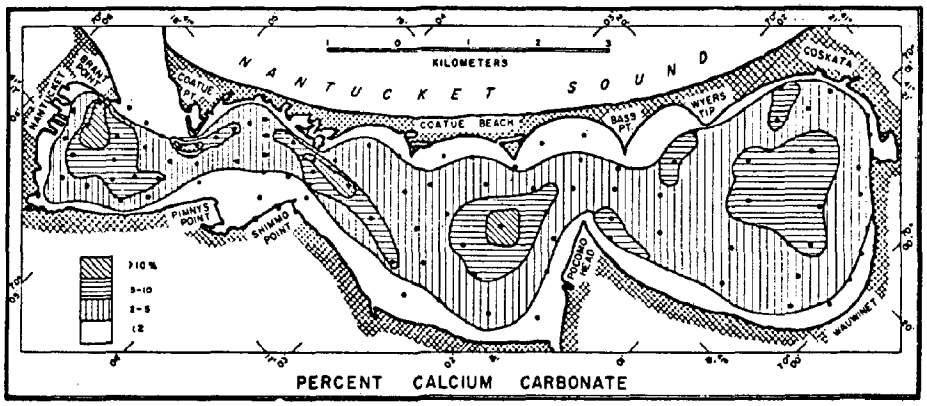
Refraction and transport patterns resulting from restrictions caused by extended shoals.

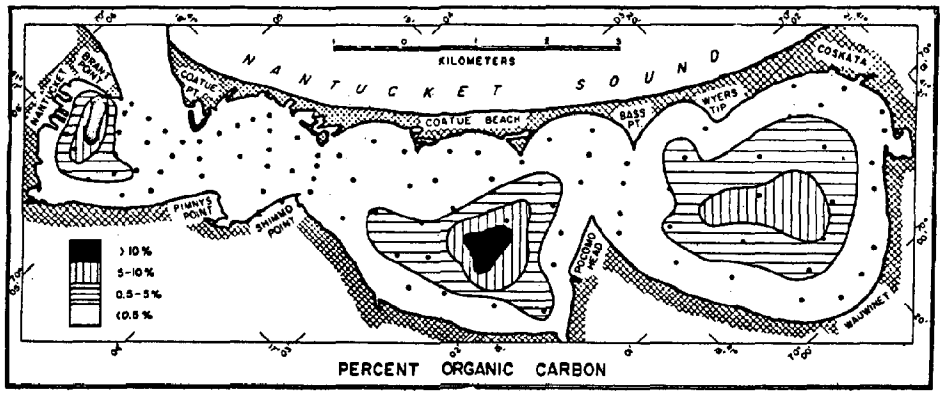


Bottom topography of Nantucket Bay revealing areas of shoals, channels, and depressions.

Fig. 1. Characteristics of tidal estuary on Nantucket Island, Mass. (Lidz, 1965).

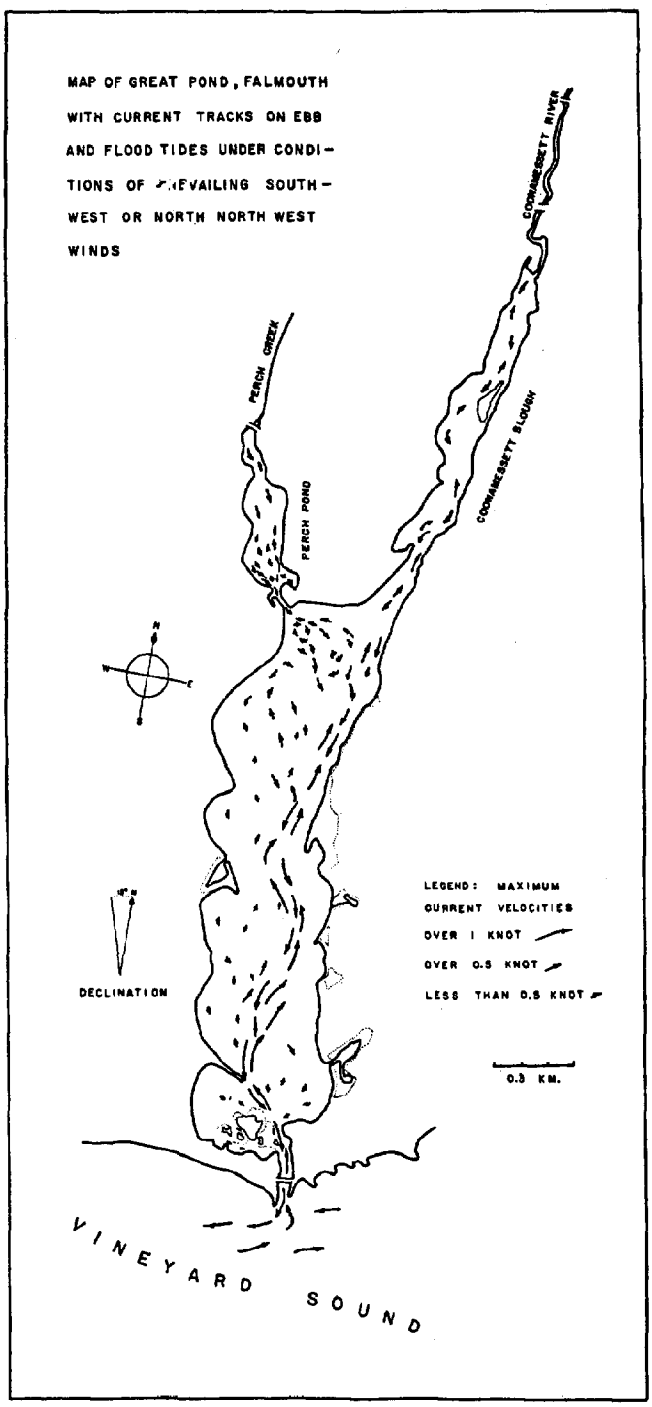






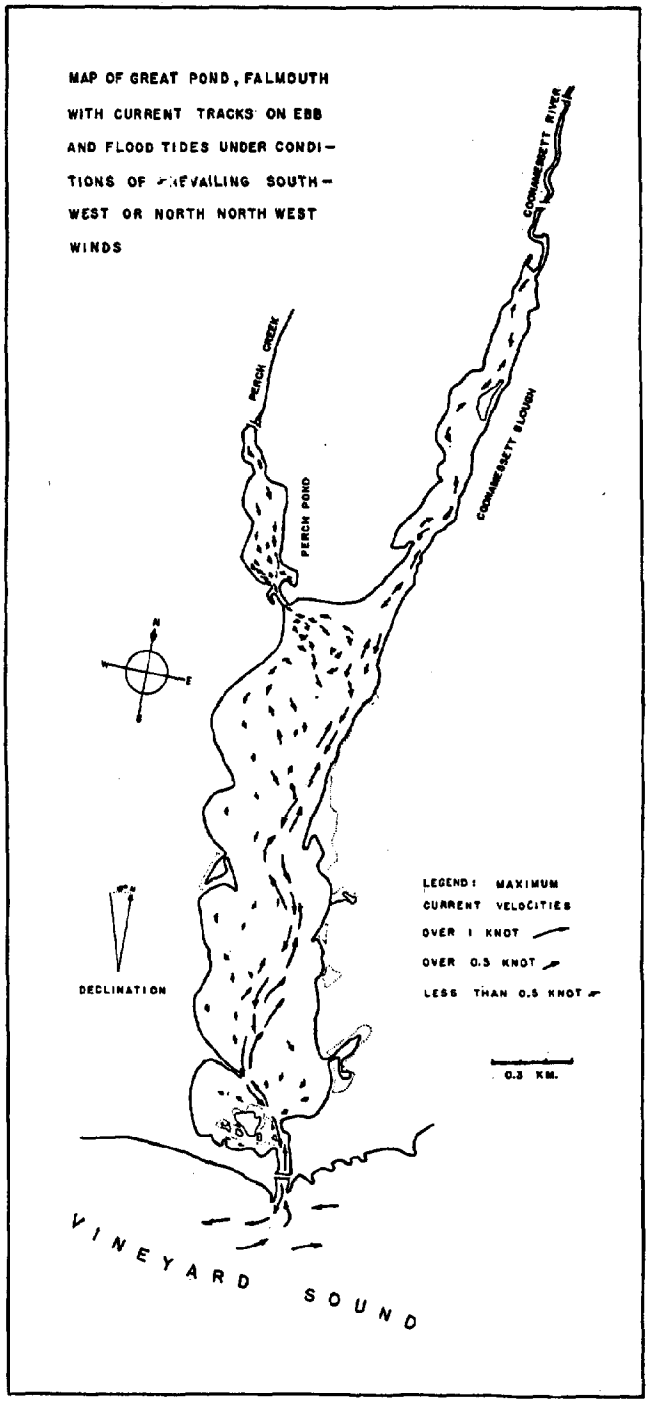
FIGS. 5, 6, and 7. Mean diameter (Fig. 5), calcium carbonate contents (Fig. 6), and % organic carbon (Fig. 7) reveal characteristic relationships between grain size and sediment composition. High values of organic carbon are found in fine-grained areas along with considerable numbers of foraminiferal tests, which raise calcium carbonate contents. Coarse sediments of channels are composed of large amounts of shell debris swept in by tidal currents.

Fig. 2. Sedimentary properties in Nantucket Bay, Mass. (Lidz, 1965).



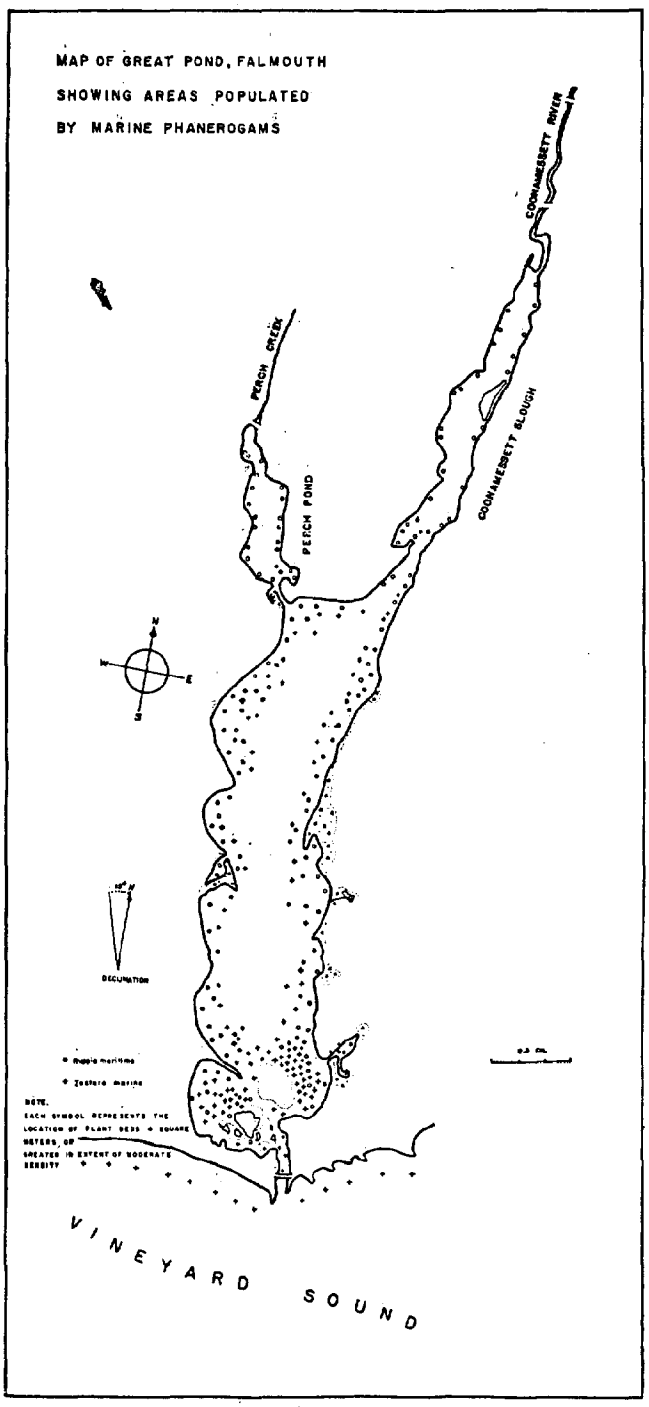
Map of Great Pond, Falmouth with current tracks on ebb and flood tides under conditions of prevailing southwest or north northwest winds. Maximum current velocities are indicated by arrows.

Fig. 3A. Tidal currents in a Massachusetts Salt Pond (Conover, 1958)



Map of Great Pond, Falmouth with current tracks on ebb and flood tides under conditions of prevailing southwest or north northwest winds. Maximum current velocities are indicated by arrows.

Fig. 3B. Tidal currents in a Massachusetts Salt Pond (Conover, 1958).



Map of Great Pond, Falmouth, Mass., showing areas populated by marine phanerogams.

Fig. 3C. Bottom vegetation in a Massachusetts Salt Pond (Conover, 1958).

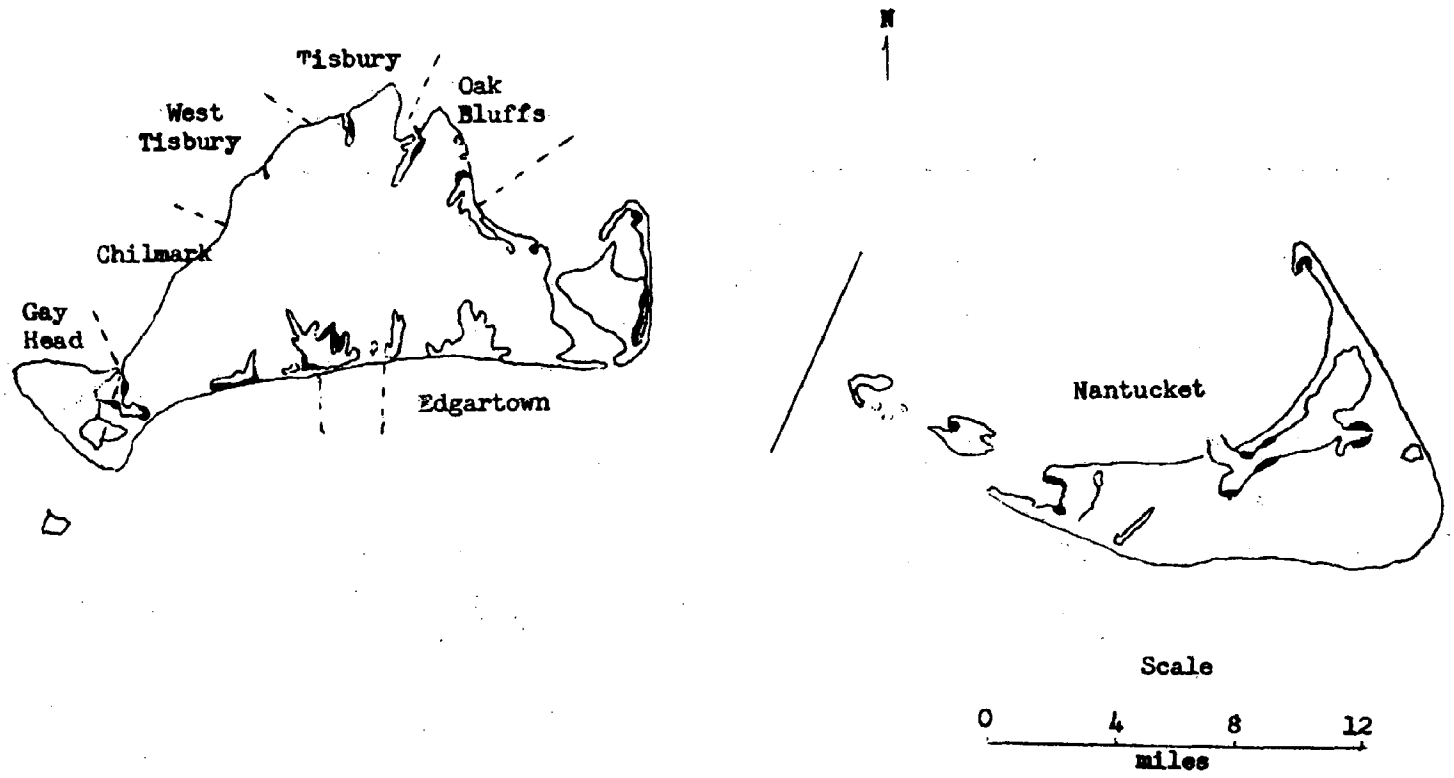
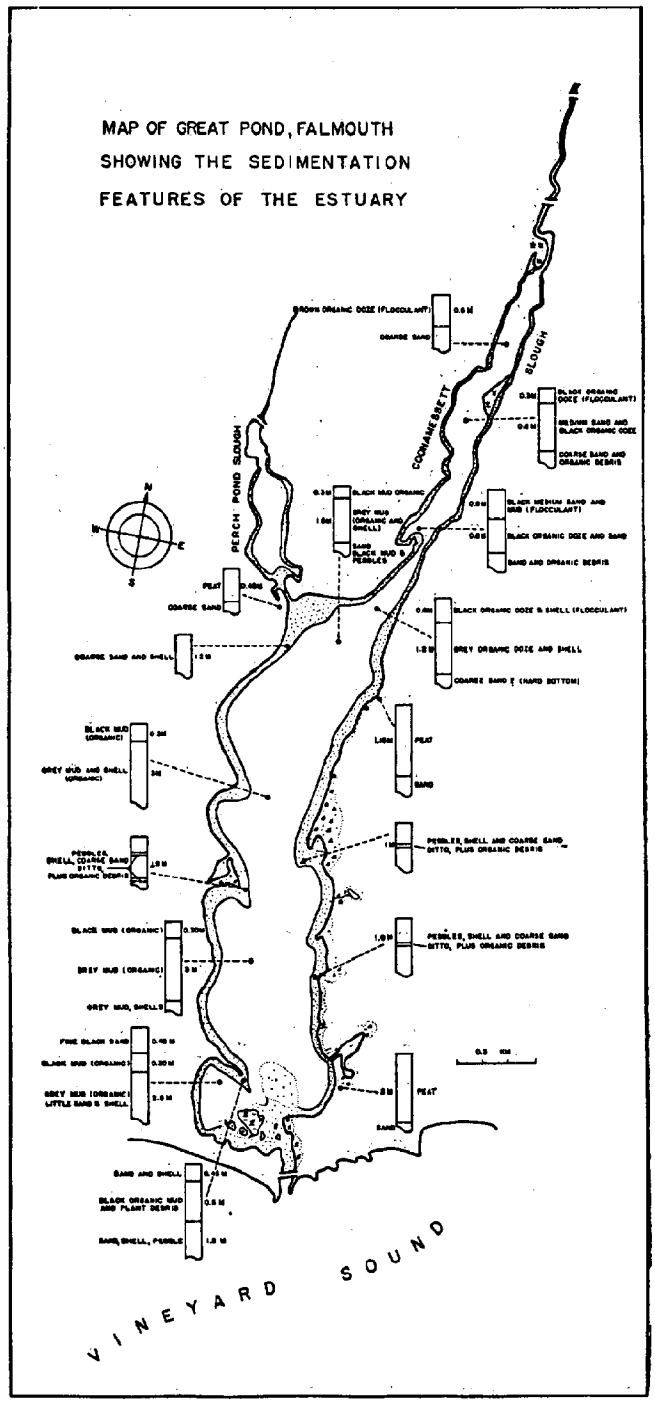
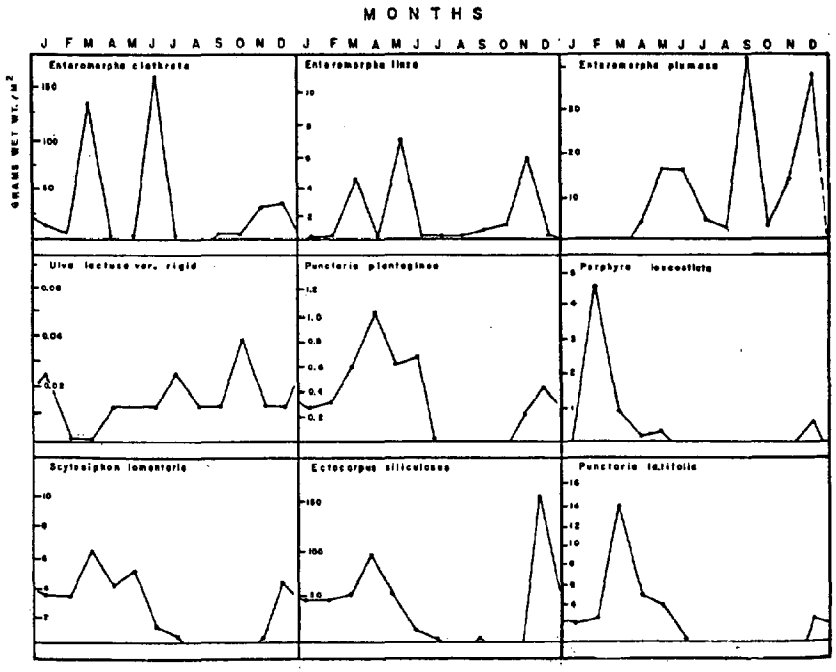


Fig. 4. Salt Ponds on Martha's Vineyard and Nantucket, Massachusetts with low salinity soft shell clam beds marked (Massachusetts Division of Marine Fisheries. Annual Report for 1964.)



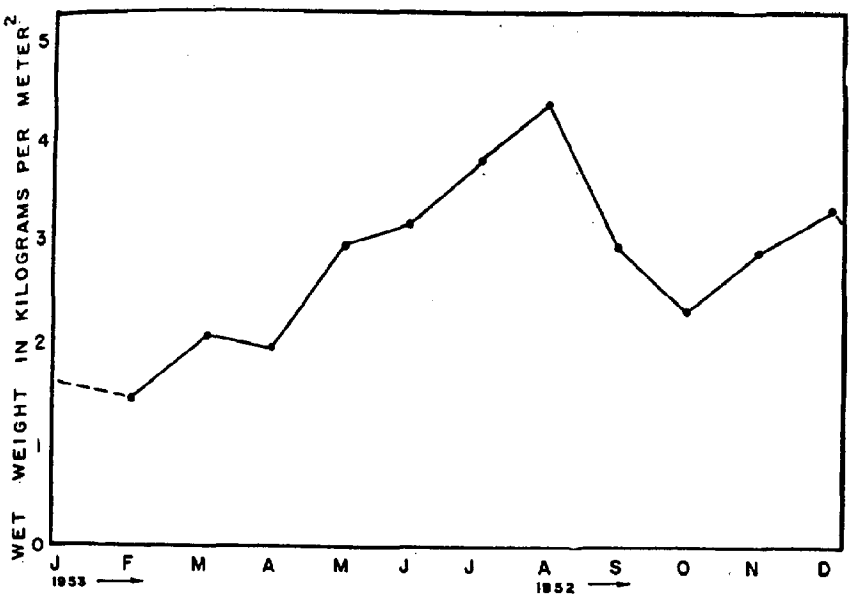
Map of sediments of Great Pond based on unpublished data by Butcher.

Fig. 5. Sediments in a Massachusetts Salt Pond (Conover, 1958).



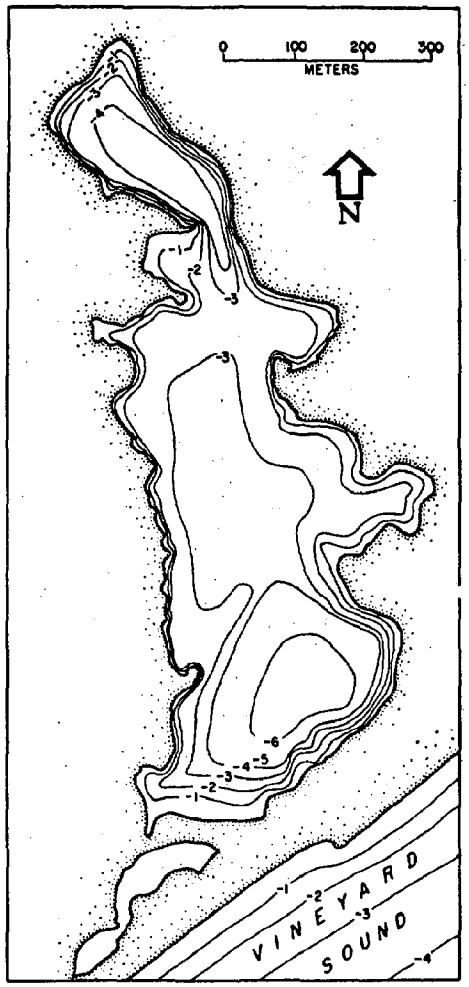
Standing crops of some benthic plants seasonally dominant in the fall and winter period in 1952–53. Data are given in grams wet weight per square meter.

Fig. 6. Seasonal succession among bottom plants in Great Pond, Mass. (Conover, 1958).

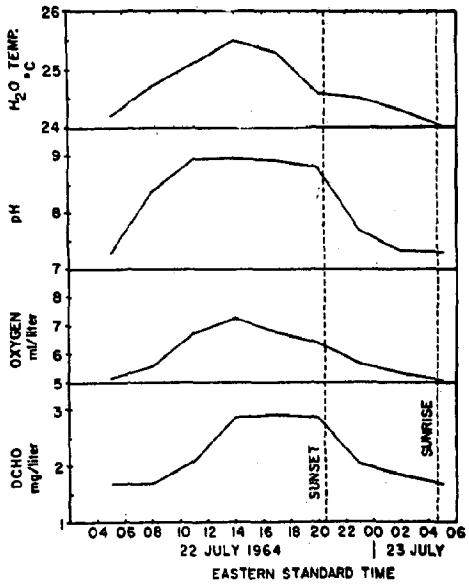


Seasonal fluctuations in the total standing crop of benthic marine plants in Great Pond in 1952–53. Data are given in kilograms wet weight per square meter.

Fig. 7. Seasonal record of mass of bottom vegetation in a Massachusetts Salt Pond (Conover, 1958).

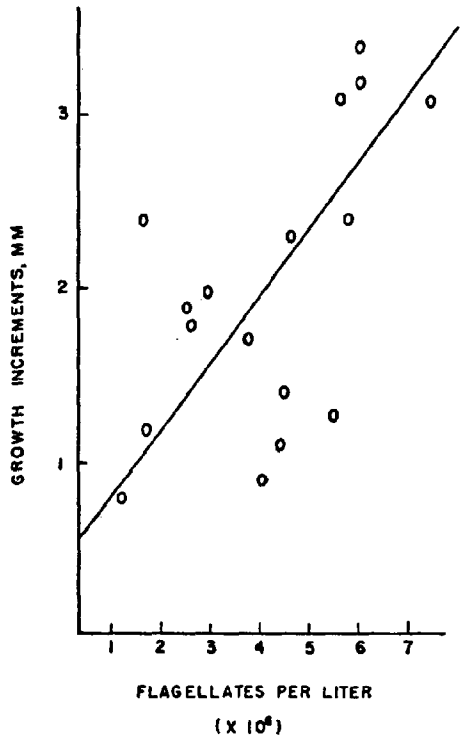


Bathymetric contours in meters of Oyster Pond (from K. O. Emery, personal communication).



Diurnal fluctuation of dissolved carbohydrate, dissolved oxygen, *p*H, and temperature in inshore water of Oyster Pond, 22 July–23 July 1964.

Fig. 8. Characteristics of a low salinity salt pond in Massachusetts (Walsh, 1965).

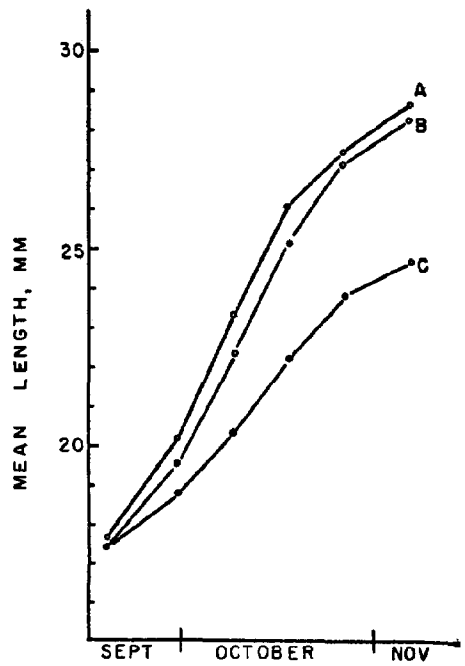


Increments of clam growth at Stations 1, 2A, 5 and 7 in Oyster Pond, determined at 10-day intervals during fall of 1958, plotted against average flagellate abundance at each station during the corresponding interval.

Fig. 9. Growth rates of soft clams (Mya) in a Massachusetts salt pond (Matthiessen, 1960b).

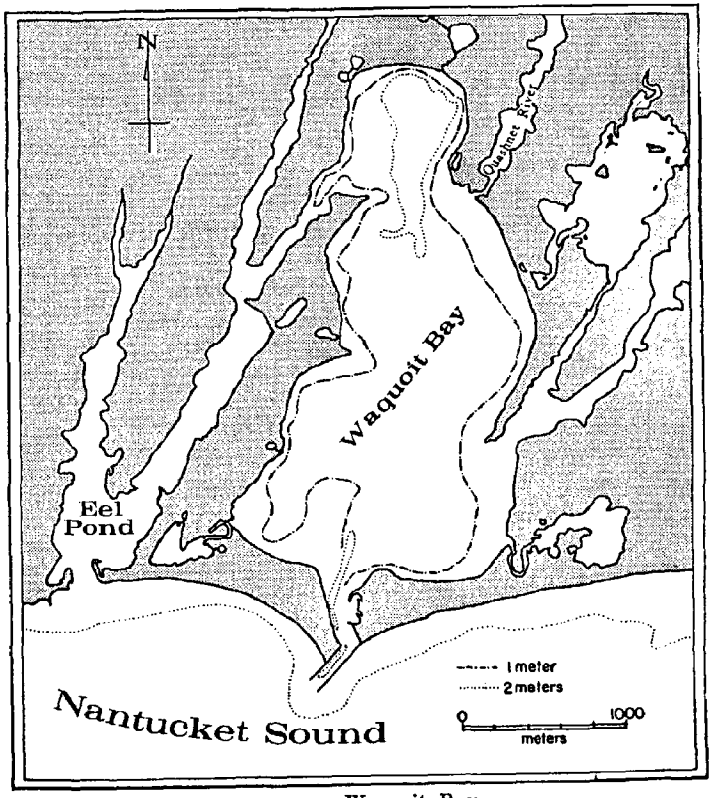
A comparison of the abundance of diatoms, flagellates, and organic detritus at Stations 2A and 7 in Oyster Pond during the period September 18–November 6, 1958

	Diatoms Cells/L × 10^6		Flagellates Cells/L × 10^6		Organic detritus cc/L	
	Sta. 2A	Sta. 7	Sta. 2A	Sta. 7	Sta. 2A	Sta. 7
Sept. 18	0.2	0.4	1.9	2.2	0.10	0.35
Sept. 22	1.0	0.5	1.3	3.9	0.30	0.20
Sept. 24	2.1	1.2	1.3	5.8	0.15	0.30
Sept. 26	1.8	1.4	1.7	10.0	0.05	0.35
Sept. 29	1.1	0.9	2.4	6.0	0.05	0.10
Oct. 1	1.0	0.9	1.8	6.5	0.02	0.15
Oct. 3	0.9	0.7	3.2	6.5	0.05	0.05
Oct. 6	0.7	0.6	3.3	5.5	0.02	0.05
Oct. 8	0.9	0.6	2.2	6.8	0.01	0.25
Oct. 10	4.4	2.1	1.8	6.3	0.02	0.10
Oct. 13	1.0	0.4	2.9	6.6	0.10	0.05
Oct. 15	1.0	0.5	2.9	11.6	0.02	0.35
Oct. 17	0.8	0.1	4.5	6.0	0.02	0.05
Oct. 20	0.7	0.2	1.3	2.0	0.05	0.05
Oct. 22	0.4	0.1	1.8	5.7	0.10	0.05
Oct. 24	0.4	0.3	2.2	5.3	0.05	0.20
Oct. 26	0.2	0.2	2.5	3.0	0.05	0.05
Oct. 28	0.3	0.3	4.1	6.0	0.05	0.20
Oct. 30	0.1	0.1	4.6	4.8	0.03	0.15
Nov. 1	0.2	0.1	5.1	5.7	0.02	0.20
Nov. 3	0.1	0.1	4.9	8.2	0.05	0.10
Nov. 5	0.1	0.1	3.4	4.7	0.02	0.03
Mean values	0.9	0.5	2.8	5.9	0.06	0.15

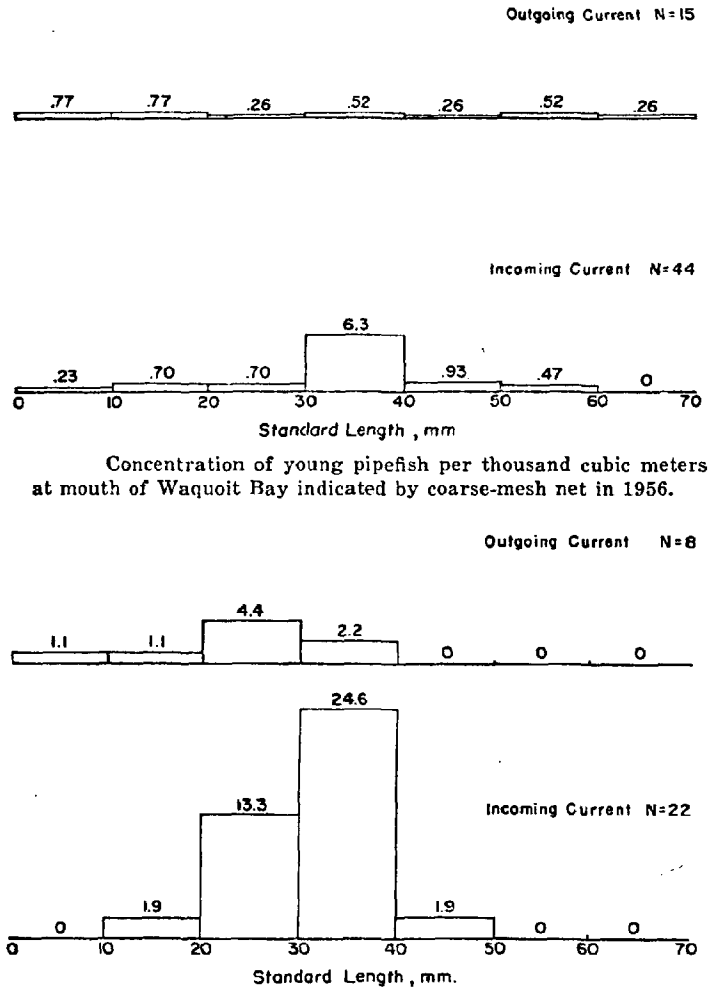


Comparison of clam growth rates at Stations 2A, 5 and 7 in Oyster Pond during period of September 18 to November 5, 1958. A = Station 7; B = Station 5; C = Station 2A.

Fig. 10. Autumn bloom of plankton in a low salinity salt pond in Massachusetts (Matthiessen, 1960b).



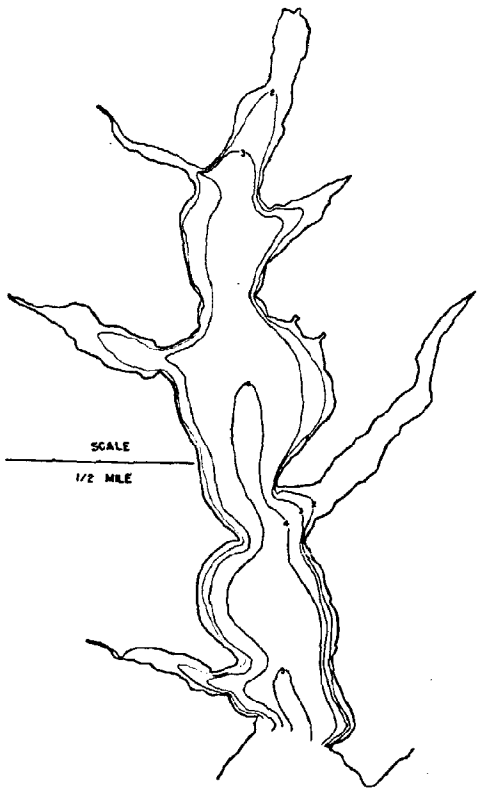
Waquoit Bay.



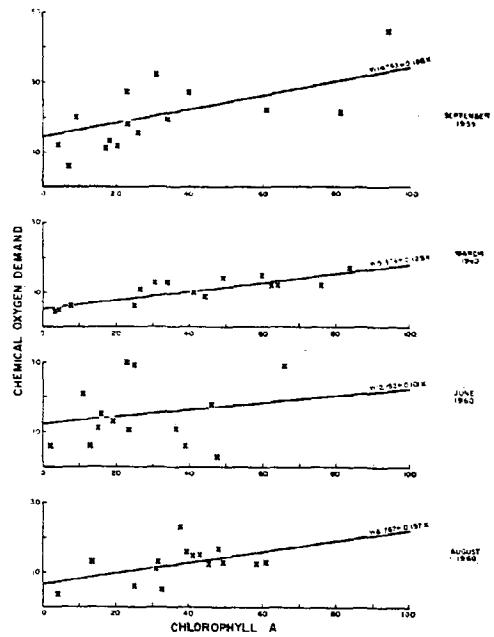
Concentration of young pipefish per thousand cubic meters at mouth of Waquoit Bay indicated by coarse-mesh net in 1956.

Concentration of young pipefish per thousand cubic meters at mouth of Waquoit Bay indicated by coarse-mesh net in 1958.

Fig. 11. Counts of young pipefish entering and leaving a salt pond in Massachusetts (Williams, G. C., 1960).



Bathymetric chart of Forge River. Outline from aerial photograph and depths in feet below mean sea level from soundings made in 1959.



Relationship between chemical oxygen demand and chlorophyll *a* in Forge River.

Fig. 12. Photosynthetic production characteristics in a salt pond (Barlow, Lorenzen, and Myren, 1963).

Tables 1-3. Relative contributions of inflowing organic matter and resident photosynthetic production in a salt pond (Barlow, Lorenzen and Myren, 1963).

Table 1. *Rates of production and consumption of oxygen in Forge River (mg $O_2/m^2/day$)*

	Gross O_2 production mg/m²/day	Not including bottom			Including bottom		
		O_2 consumption	Net change	Ratio P/R	O_2 consumption	Net change	Ratio P/R
March 1959	1,050	690	+360	1.52	1,200	−160	0.87
June	3,820	5,800	−2,000	0.66	6,320	−2,520	0.60
Aug	10,000	16,900	−6,900	0.59	17,420	−7,420	0.57
Sept	4,400	9,700	−5,300	0.45	10,220	−5,820	0.43
March 1960	7,420	4,780	+2,640	1.55	5,300	+2,120	1.40
June	9,075	9,240	−165	0.98	9,760	−685	0.93
Aug	14,025	15,000	−975	0.93	15,520	−1,500	0.90
Sept	7,750	5,280	+2,470	1.47	5,800	+1,950	1.34
March 1961	5,440	10,230	−4,970	0.53	10,750	−5,310	0.51
			mean P/R ratio	0.96		mean P/R ratio	0.84

Table 2. *River flow and accumulated fresh water in Forge River*

Survey	River flow per day R	Accumulated fresh water Q	Exchange ratio r
	(10^6 ft³)		
C Aug 59	0.56	9.42	0.06
D Sept 59	0.56	4.93	0.11
E Mar 60	2.47	5.37	0.46
F June 60	0.76	5.45	0.14
G Aug 60	0.68	6.23	0.11
H Sept 60	0.70	7.06	0.10
I Mar 61	1.05	3.70	0.28
K June 61	0.51	3.57	0.14
L July 61	0.92	7.04	0.12

Table 3. *Processes determining the accumulation of organic matter in Forge River. Means are weighted according to the volume distribution in the estuary*

Date	BOD from river (mg/day × 10^6)	Exchange ratio (r)	Mean respiration rate (mg O_2/L/day)	Daily destruction coefficient e^k	BOD from river accumulated (mg O_2 × 10^6)	Per cent accumulated of total BOD	Per cent respiration accounted for by BOD from river	Mean chlorophyll a (mg/m³)
Aug 59	720	0.06	14.6	0.86	224	0.2	7.5	42
Sept 59	560	0.11	8.4	0.90	314	0.6	10	30
Mar 60	910	0.46	3.2	0.94	1,420	5.1	13	34
June 60	980	0.14	6.7	0.88	559	2.0	21	25
Aug 60	890	0.11	10.9	0.86	422	0.8	12	39
Sept 60	730	0.10	5.2	0.94	473	0.8	20	49
Mar 61	1,540	0.28	9.2	0.83	1,537	3.2	21	26
June 61	1,000	0.14	9.4	0.91	652	1.0	15	49
July 61	1,360	0.12	10.0	0.84	663	2.1	20	

Chapter C-8

OLIGOHALINE REGIME

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INTRODUCTION

The distinctive system existing at the river mouth-estuarine area of most temperate estuaries is unique in many ways. The unidirectional flow of the river changes to the slowly mixing circulation of a wide shallow body of water, representing a change in energy from flow to circulation. The water is characteristically turbid and contains large amounts of silt materials coming in from the river. The bottoms are dominated by grass and filtering clams (Rangia cuneata in the southern temperate zone and Mya arenaria in the northern temperate zone, with some overlap in the intermediate zones).

The species diversity of the flooding system is relatively low. Because these rivers flow strongly at times, there are sudden fluctuations in salinity. It is this sudden change as much as the low level which eliminates many species. Those species that survive apparently possess adaptive abilities to divert part of their energies to salinity and turbidity adaptations.

Nutrient and organic detritus transported into the system is dependent on the source and volume of flood waters via the contributing streams. After extensive flooding, for example, the river water is relatively poor in nutrient and organic matter.

These systems manage to consume and produce at high levels in spite of the heavy import-export flux, light-absorbing turbidity and salinity shocks. According to Odum (1967b) populations of Rangia may exceed 12 per square foot in some areas. With a large filtering rate, imported organics are captured, minerals are released from the imports and waters are cleared by aiding floculation, all of which provide a regenerative feedback of minerals to the phytoplankton.

SYSTEM EXAMPLES

Pamlico River Estuary, North Carolina

A wide range of studies has been in progress since 1965 in the Pamlico River estuary (Figure 1) under the auspices of the North Carolina State University Estuarine Research Station, from whom data were made available for this report. The major part of the estuary constitutes a typical oligohaline system in which salinity is normally less than 10 ppt.

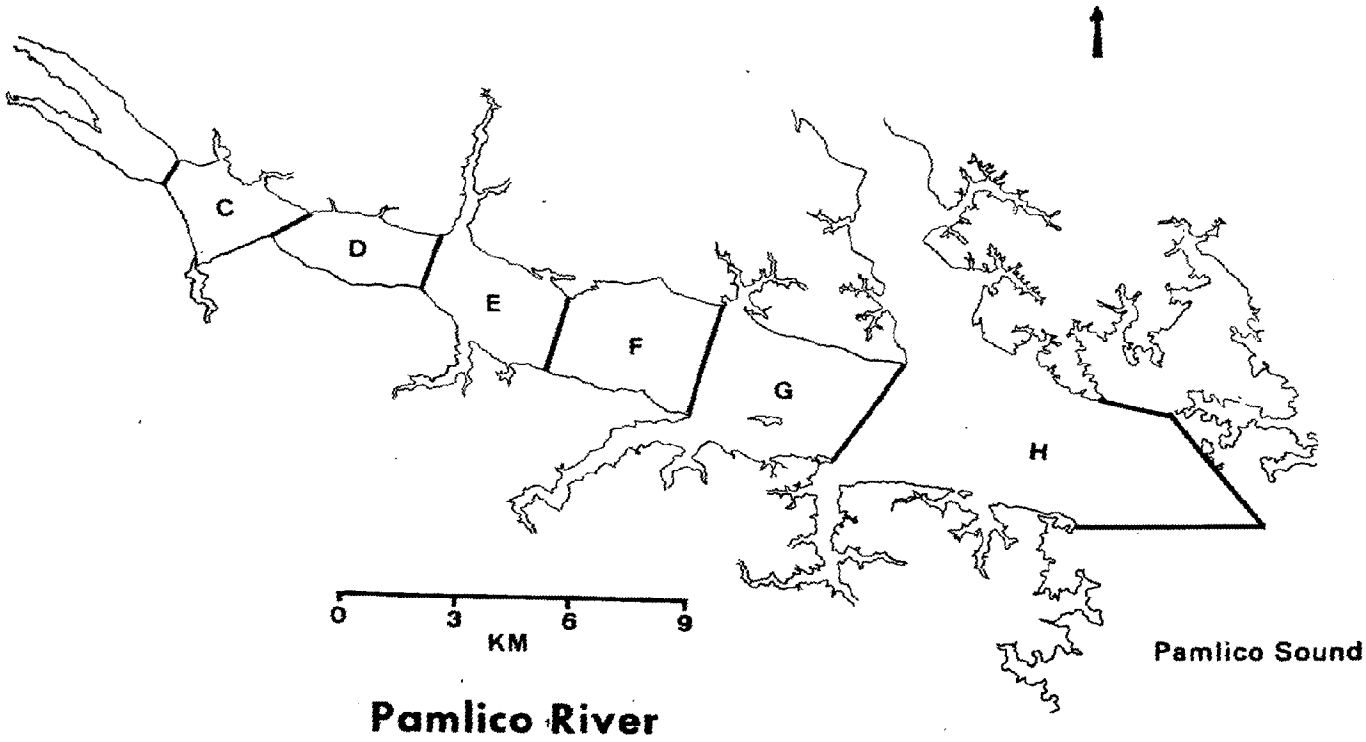


Fig. 1. Pamlico River estuary, North Carolina. Collecting areas are indicated by letters.

The estuary is characterized by low salinity, high turbidity and shallow water. Some of the important energy transfers have been deduced and are shown in a simplified diagram in Figure 2. The more abundant and characteristic organisms in the system are named rather than using broad general classification. For example, dinoflagellates and Acartia tonsa dominate the phytoplankton and zooplankton, respectively.

Because the estuary is shallow and the deeper waters are frequently low in dissolved oxygen during the summer, most of the benthic invertebrate species occupy the sandy, nearshore sediments. These shallow waters of low salinity have dense stands of Ruppia with attached periphytic algae and associated animals, particularly rotifers, polychaetes, nematodes, gammarid amphipods and grass shrimp (Paleomonetes sp.). The approximate limits of distribution of the dominant infaunal benthic invertebrates in the estuary are shown in Figure 3. Seasonal distribution of the benthic components of the Pamlico River Estuary is outlined in Table 1 from the stations indicated in Figure 4. Of the two dominant species, Macoma balthica appears to be ubiquitous, whereas Rangia cuneata is restricted to the oligohaline portion of the estuary. In a recent study, Tenore et al., (1968) demonstrated that Rangia receive a major part of their nutrition from organic matter in the substrate, which may be a function of input from the river.

The estuary is protected by Pamlico Sound and the outer banks so that the diurnal tidal amplitude averages less than 20 cm. The flushing rate is correspondingly low (Table 2) and entrained particles tend to remain in the estuary for long periods of time. The estuary is unusually shallow, averaging about 1.5 m with average deep water about 5 m. Although shallow, the deeper water sediments are primarily fine silt and clays which may act as a nutrient trap (Davis 1968). Salinity is low in the spring and increases to maximum values in the fall or winter (Figure 5). Changes in salinity seasonally seems to be associated with variation in fresh water runoff as suggested by Roelofs and Bumpus (1953). Williams and Deubler (1968) indicated that this general salinity cycle is characteristic of North Carolina estuaries. The plankton based system of Pamlico Sound replaces much of the oligohaline system of Pamlico River during the fall and winter months. However, during the more productive time of the year, the system is essentially oligohaline, particularly in the shallow water where most of the species exist. The more or less permanent oligohaline system lies westward of Indian Island (Figure 1, G). Typically, a zone of reduced dissolved oxygen develops in the bottom 1 m of the water column during periods of the summer. This zone, occupying the general area between areas E & G, is brought about by a combination of thermohaline vertical stratification (e. g. Fig. 5B), a high surface turbidity and reduced wind stress. If these conditions persist for a period of time, dissolved oxygen concentration falls, often below 1 mg/l. This characteristic of Pamlico River is held responsible by K. R. Tenore (personal communication) for the virtual absence of macro-benthic invertebrates from the deeper water sediments. Macoma balthica does occur, but may suffer severe mortalities in years when dissolved oxygen concentrations drop to particularly low values or persist for relatively long periods of time. During the summer of 1966 an extensive fish kill occurred along the north shore of the estuary when a strong northeasterly wind followed a two week period of calm weather, and

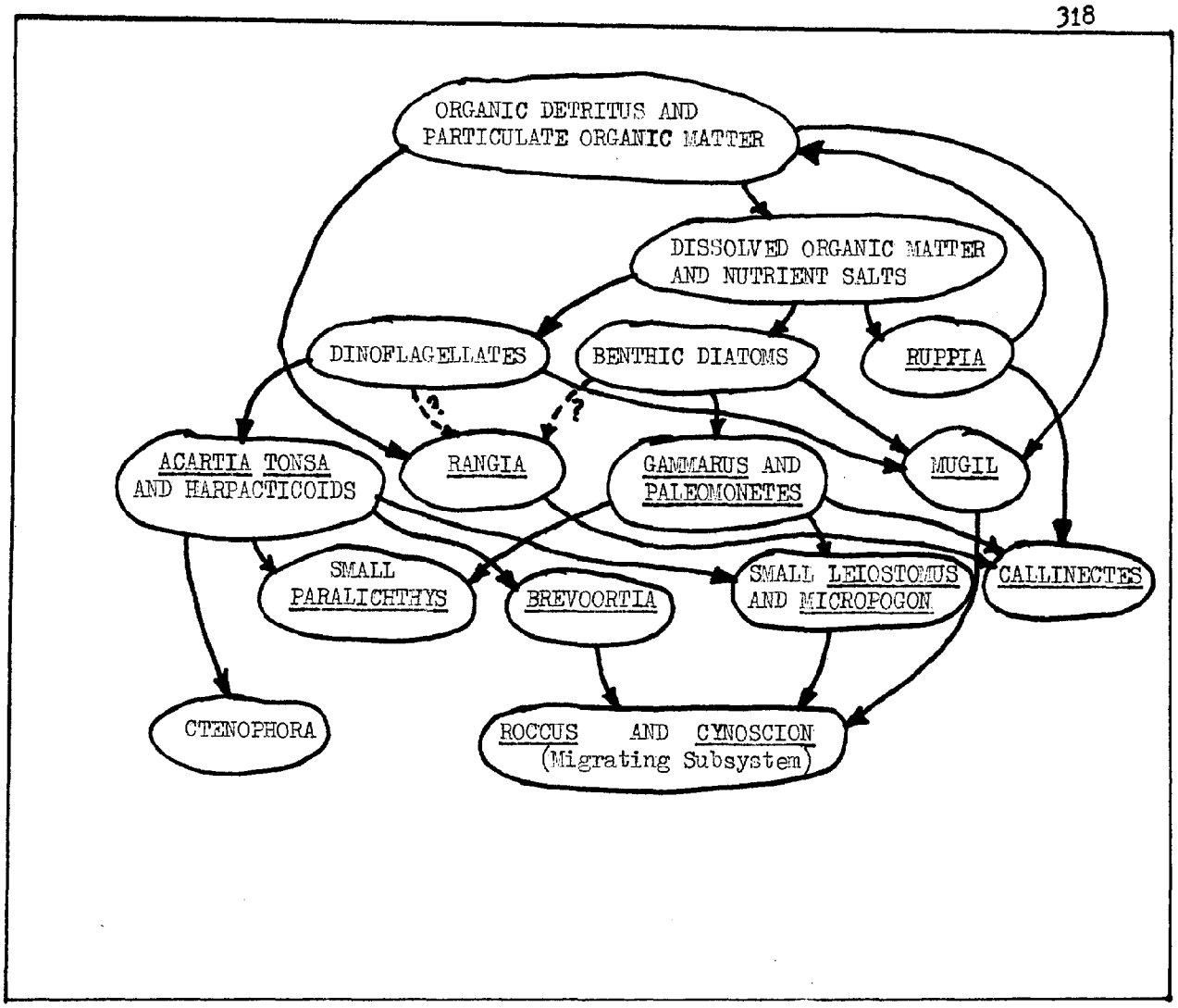


Fig. 2: Simplified diagrammatic representation of major food web components in the oligohaline system, Pamlico River Estuary, N. C.

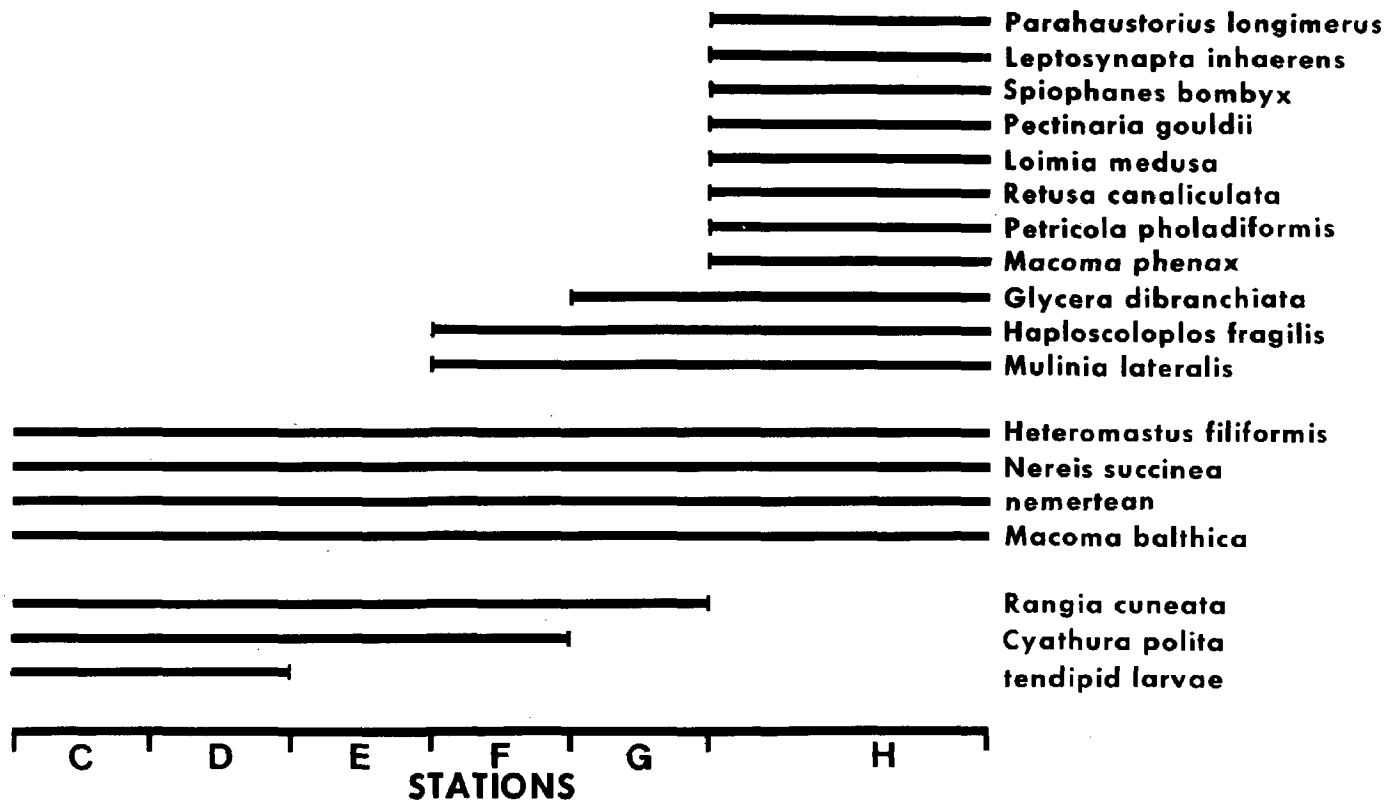


Fig. 3A. Dominant and characteristic macro-benthic species in Pamlico River estuary, North Carolina (From Tenore, 1970). See Fig. 1 for Stations.

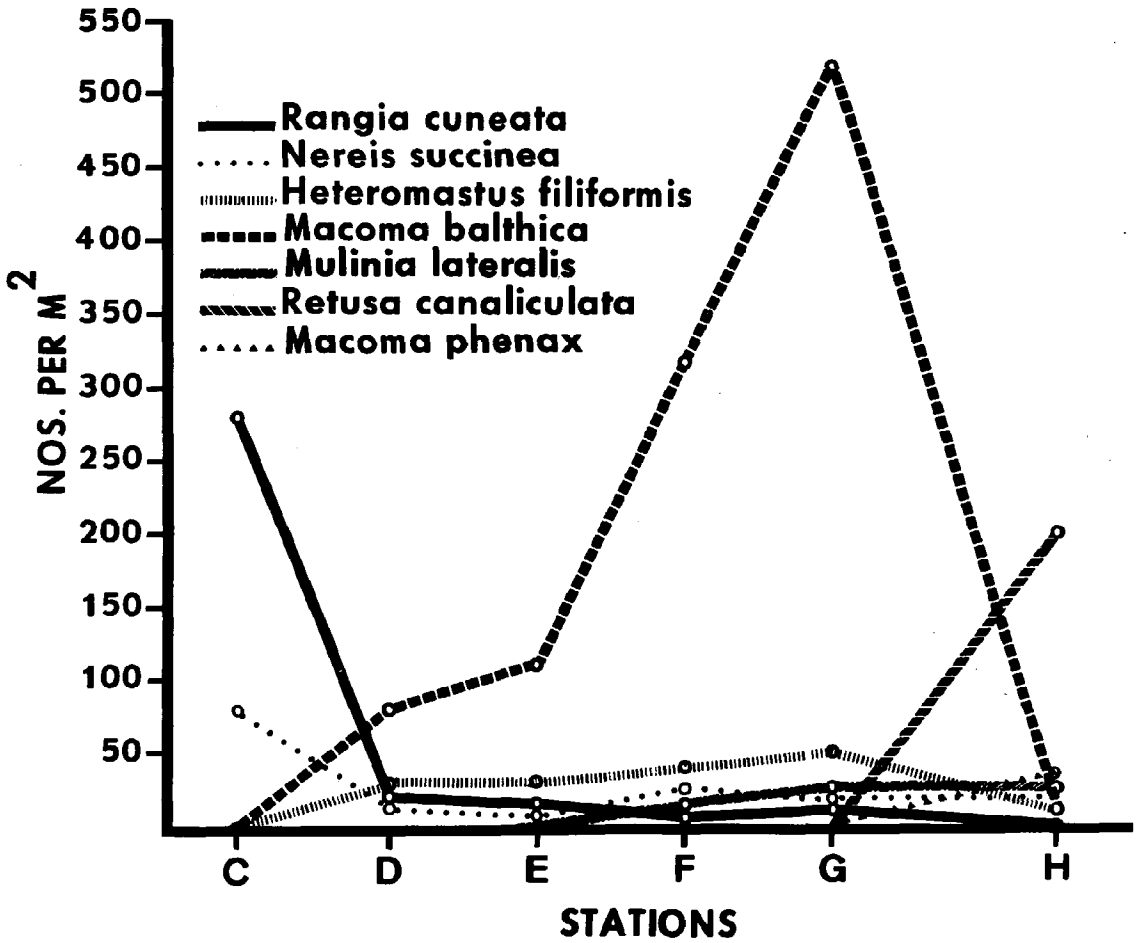


Fig. 3B. Distribution of biomass of the dominant macro-benthic species in Pamlico River estuary, North Carolina (From Tenore, 1970). See Fig 1 for station locations.

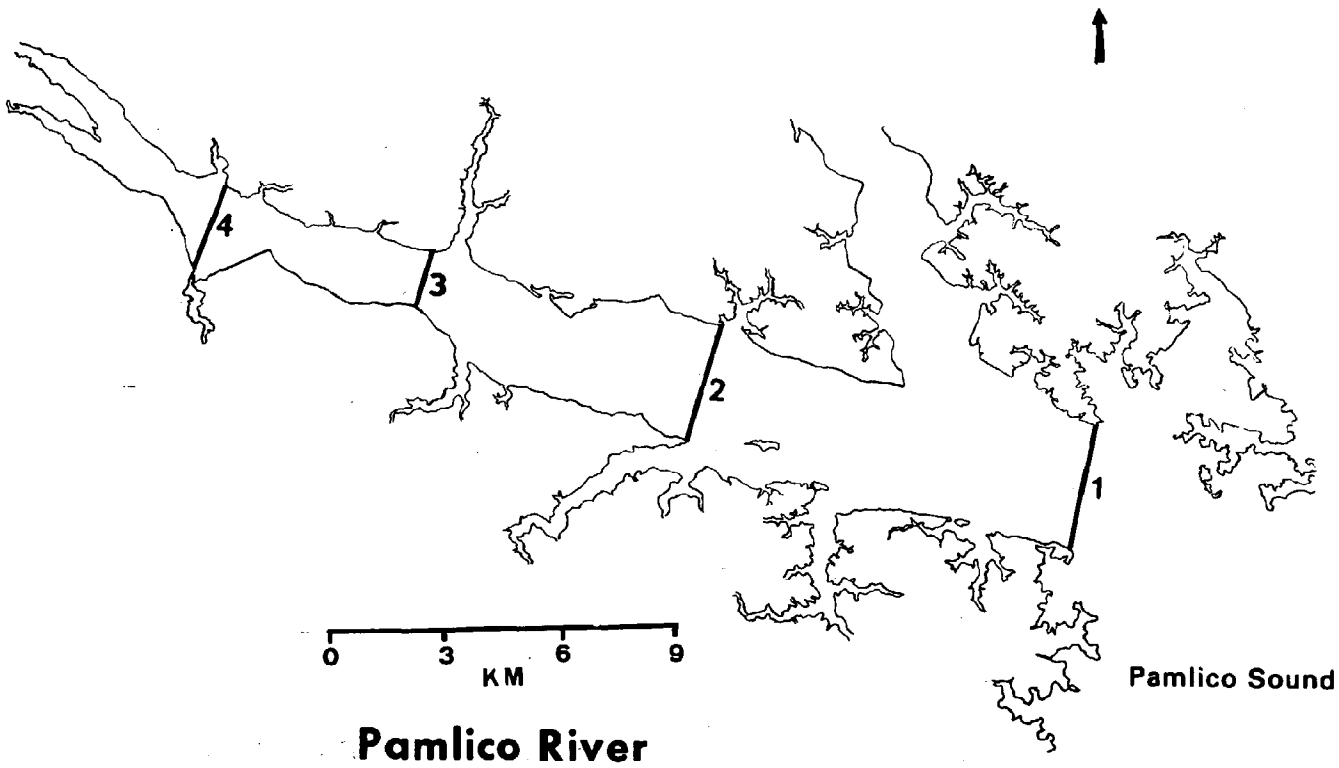


Fig. 4. Sampling areas in the Pamlico River estuary for the seasonal changes reported in Table 1 (From Tenore, 1970).

Table 1. Seasonal changes in the distribution of benthic species in the Pamlico River estuary (From Tenore 1970).

species	fall				winter				spring				summer			
	1	2	3	4*	1	2	3	4	1	2	3	4	1	2	3	4
Cyathura polita	+	+	+	+	-	-	+	+	-	+	+	+	-	+	+	+
Rangia cuneata	-	+	+	+	-	+	+	+	-	+	+	+	-	+	+	+
Nereis succinea	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
nemertean a	+	+	+	+	+	+	+	-	+	+	+	-	+	+	+	+
Macoma phenax	+	+	+	-	+	+	+	-	+	+	+	-	+	+	+	-
Macoma balthica	-	+	+	-	-	+	+	-	+	+	+	+	+	+	+	-
Heteromastus filiformis	+	+	+	-	+	-	-	-	+	+	+	+	+	+	+	+
Mulinia lateralis	+	+	+	-	+	+	+	-	+	+	+	-	+	-	-	-
Haploscoloplos fragilis	-	+	-	-	-	+	-	-	+	+	-	-	-	+	-	-
polychaete e	+	+	-	-	+	+	-	-	+	-	-	-	-	-	-	-
Lepidactylus dytiscus	-	+	-	+	+	+	+	+	+	+	+	-	-	-	-	+
Parahaustoria longimerus	-	-	-	-	+	+	+	+	+	-	-	-	+	-	-	-
Pectinaria gouldii	+	-	-	-	+	-	-	-	+	+	-	-	+	-	-	-
Glycera di branchiata	+	-	-	-	+	+	-	-	+	-	-	-	+	-	-	-
Retusa canaliculata	+	-	-	-	+	+	-	-	+	-	-	-	+	-	-	-
Leptosynapta inhaerens	+	+	-	-	+	-	-	-	+	-	-	-	+	-	-	-
Epitonium rupicola	+	-	-	-	+	-	-	-	+	-	-	-	+	-	-	-
Haminoea solitaria	+	-	-	-	+	-	-	-	+	-	-	-	+	-	-	-
Loimia medusa	+	-	-	-	+	-	-	-	+	-	-	-	+	-	-	-
Petricola pholadiformis	+	-	-	-	+	-	-	-	+	-	-	-	+	-	-	-
Sayella chesapeakea	+	-	-	-	+	+	-	-	+	-	-	-	-	-	-	-
Blanoglossus sp.	+	-	-	-	+	-	-	-	+	-	-	-	-	-	-	-
chironomid larvae	-	-	+	-	-	+	+	+	-	-	+	+	-	-	-	-
Gemma gemma	+	-	-	-	+	-	-	-	+	-	-	-	-	-	-	-
Nassarius vibex	+	-	-	-	+	-	-	-	+	-	-	-	+	-	-	-
Diopatra sp.	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-
Eteone alba	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
snail a	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Spiophanes bombyx	+	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-
Mya arenaria	-	-	-	-	+	+	-	-	+	+	+	-	-	-	-	-
Leptoplana sp.	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-
Lyonsia hyalina	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-
Mitrella lunata	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-
Brachiodontes recurvus	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
nemertean b	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-

*Collecting areas. See Fig. 4.

Table 2. Average exchange ratios and half-life values estimated for volume segments within sections of the Pamlico River estuary. Fresh water inflow averaged 42 x 10^5 m^3 / tidal cycle (99.1 m^3/ sec). (From Horton, 1967)

Section	Length of Section	Number of Volume Segments	Average Exchange Ratio	Half-life/ Segment (tides)
Washington to Rumley Marsh	28.0	3	.084	7.9
Rumley Marsh to Indian Island	10.8	2	.082	8.0
Indian Island to Pamlico Point	25.4	5	.073	9.1

Table 3. *In situ* phytoplankton C_{14} assimilation estimates at six stations in Pamlico River, August 1966 - August 1967.

Station	No. of estimates	mg C/ m^2 / day High	Low	Average	gm C/m^2/year
A	16	478	5	145	53
B	17	572	4	164	60
C	14	544	11	219	80
D	16	400	2	127	46
E	15	866	1	122	45
F	10	373	2	110	40

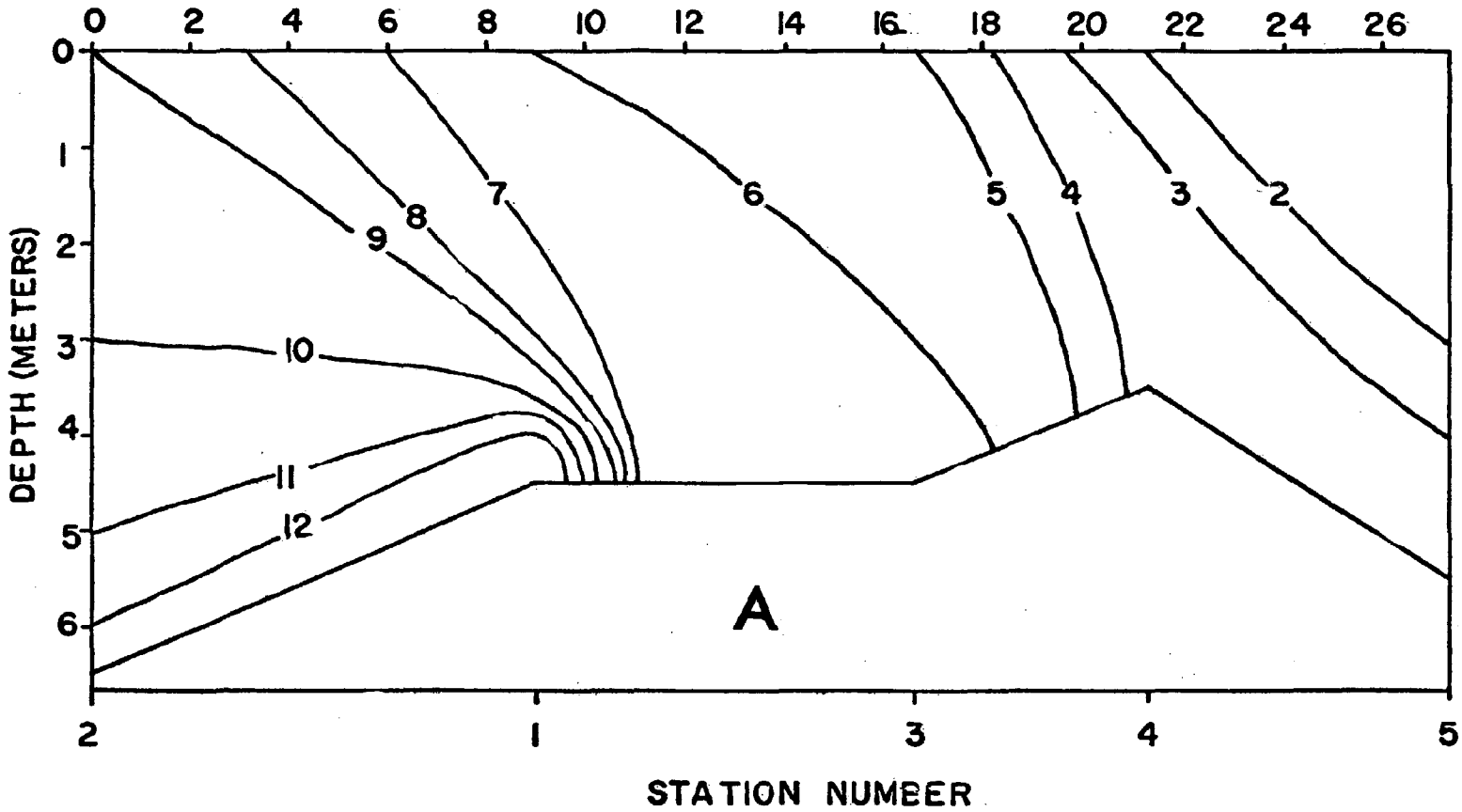


Figure 5A. Isohalines in ppt in Pamlico River, N. C. June 28, 1965.

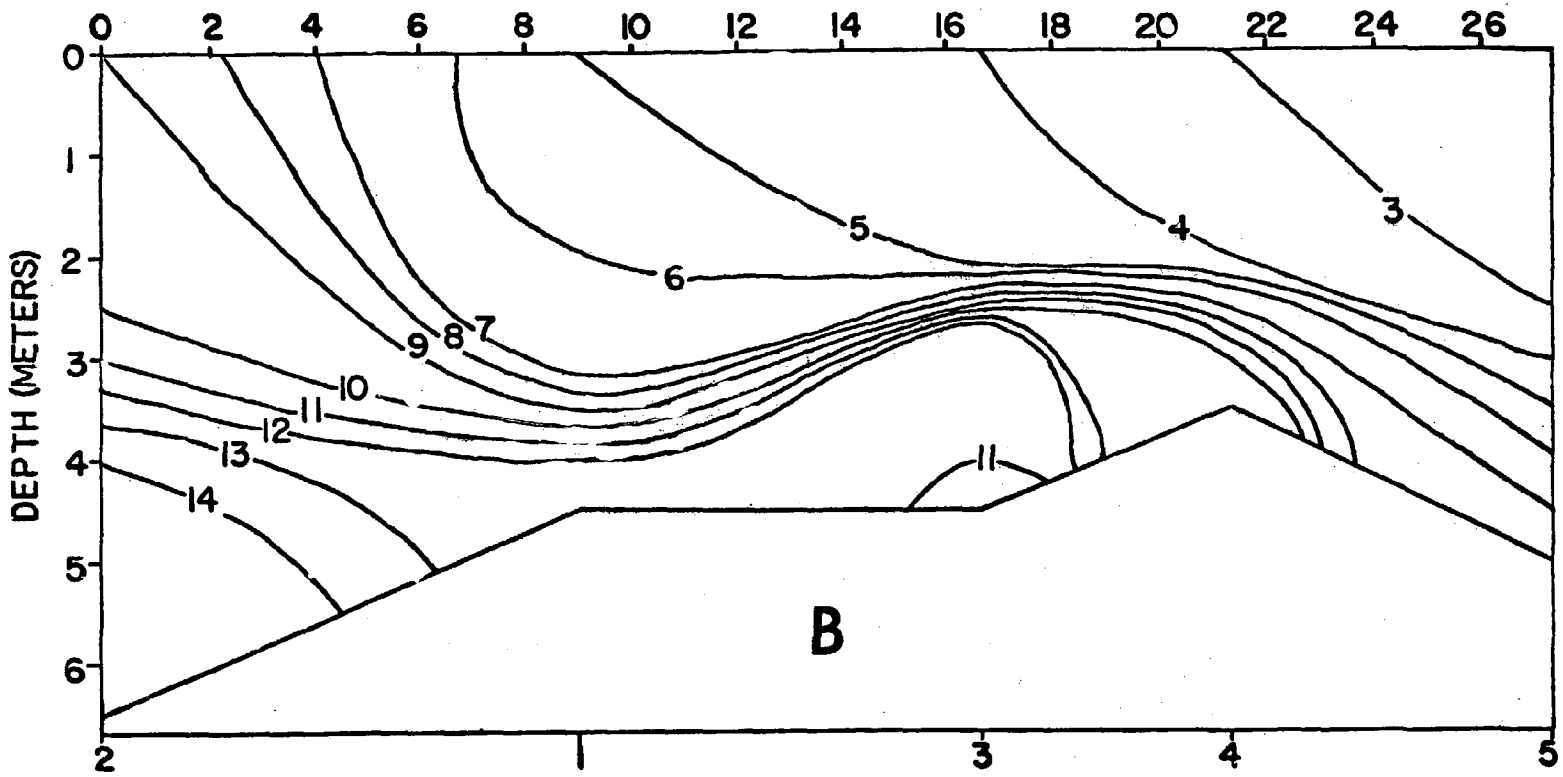


Figure 5B. Isohalines in ppt in Pamlico River, N. C. August 18, 1965.

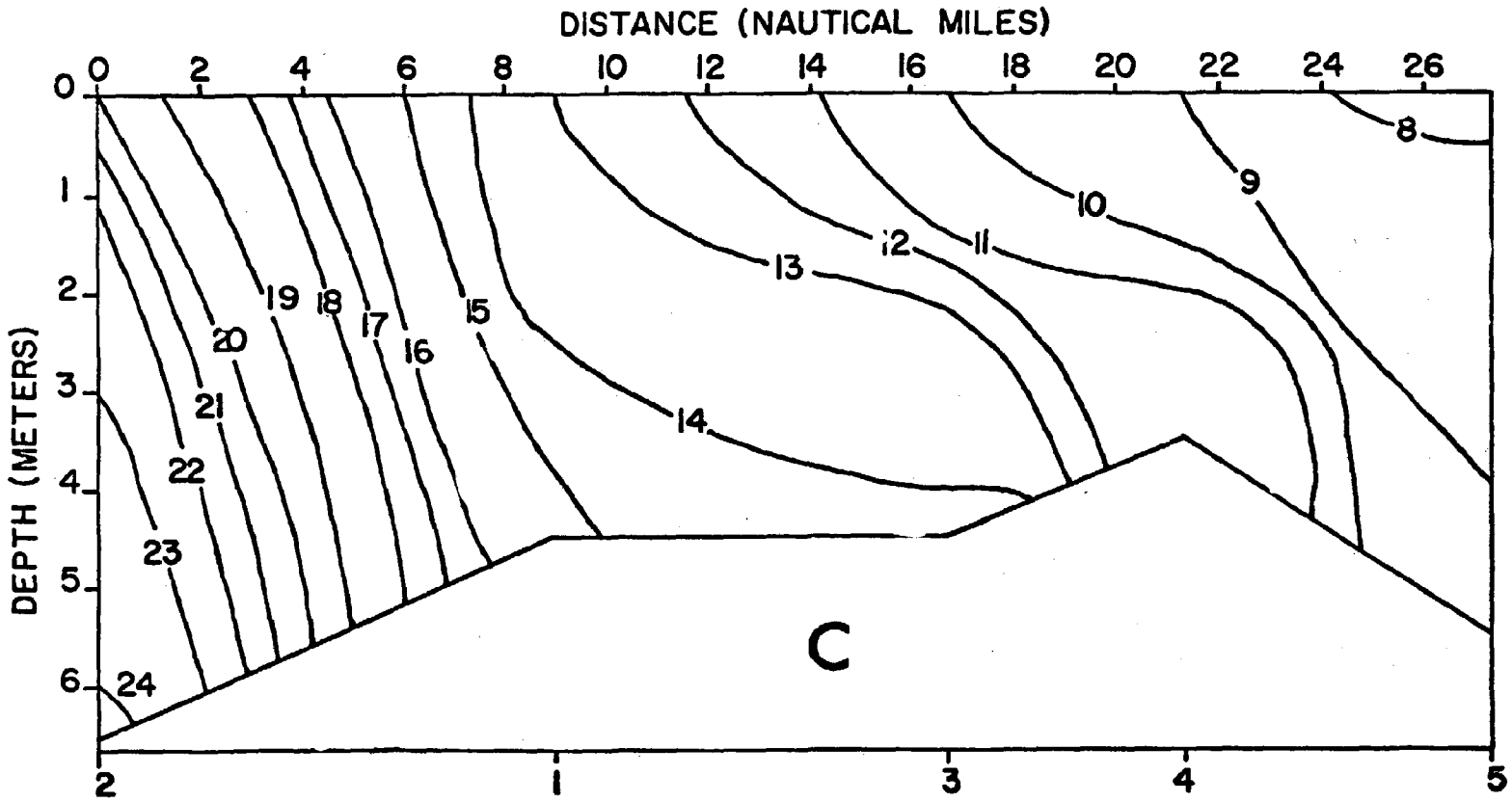


Figure 5C. Isohalines in ppt in Pamlico River, N. C. October 6, 1965.

dissolved oxygen content of the bottom water was below 1 mg/l. This water rose to replace surface wind driven water along the lee shore of the estuary. High temperatures at the surface probably also contributed to the kill.

The euphotic zone is generally restricted to the upper 2 m of the water column. This feature coupled with the shallow nature of the estuary is thought by Miller and Hobbie (MS) to be responsible for the relative scarcity of diatoms in the phytoplankton. The phytoplankton is dominated by motile dinoflagellates which would seem to have an advantage over the heavier diatoms in their ability to remain in the surface euphotic zone. In situ phytoplankton C_{14} assimilation experiments during 1967 yielded average values shown in Table 3. These averages compare favorably with data collected by Williams (1966) for nearby, but more saline environments, in North Carolina. However, there was no apparent seasonal cycle, and average values fluctuated considerable from one sampling period to the next, although there was better agreement among stations at any one time. Peak assimilation values in excess of 200 mg C/m^2/day were estimated for dates in November, January, February and June. Perhaps stormy weather, including wind mixing and accompanied by nutrient-rich rainwater (Reimold and Daiber 1967), creates conditions allowing brief bursts of phytoplankton activity. The standing crop of phytoplankton did not reflect the fluctuations in C_{14} assimilation. Biomass estimates by direct count and cell size calculations averaged less than 7 mg/l except during the period between mid-January and mid-March when peak concentrations averaged greater than 30 mg/l. This early spring bloom was attributed to a single species of dinoflagellate, Peridinium triquetrum and was studied intensively by Miller and Hobbie (MS) during the 1967-68 flowering. They suggest that the dinoflagellate bloom, which is atypical in Atlantic coast estuaries where diatoms are usually dominant during the spring flowering, is related to low salinity, high metabolite concentrations, low nutrients, shallow water or the shallow euphotic zone of the estuary. Peters (1968) showed that the seasonal cycle of particulate carbon in Pamlico River followed the same trend as did chlorophyll a concentrations (Figure 6A). This may indicate a rapid turnover of both phytoplankton and oxidizable organic matter (E. J. Kuenzler, personal communication).

In the shallow inshore waters less than 2 meters in depth, dense stands of rooted macrophytes are present. Ruppia maritima dominates this community in the typically oligohaline portions of the estuary where salinity ranges between 3 and 10 ppt, but Potamogeton sp. is also common. The blades of both species accumulate a rich epiphytic and animal biota during the growing season. A. Sherk (personal communication) has made preliminary estimates of the C_{14} assimilation of epiphytes on glass slides in the estuary. Incubations made at 600 foot-candles gave assimilation values between 0.35 and 39.3 gm C/m^2/year. These values are somewhat lower than, though in the same order of magnitude as, the phytoplankton assimilation estimates. No independent estimate of productivity by the rooted macrophytes is available, but, as is inferred from Figure 2, all three classes of primary producers are important.

Peters (1968) studied the distribution of zooplankton in the Pamlico estuary. He found Acartia tonsa to be the most abundant copepod species

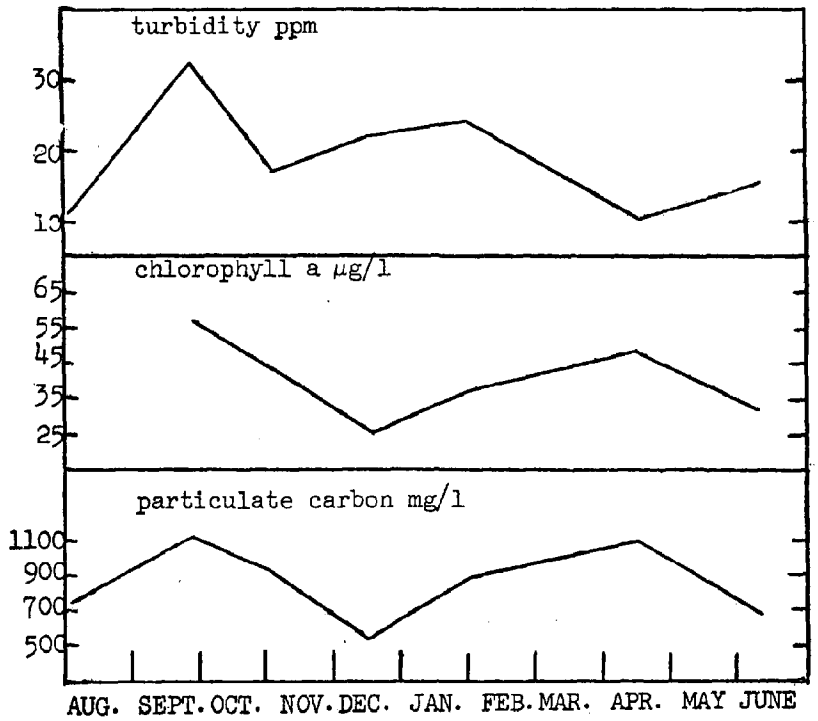


Figure 6A. Seasonal changes in turbidity, chlorophyll a and particulate carbon near Indian Island, Pamlico River, N. C. in 1966-67. (From Peters, 1968)

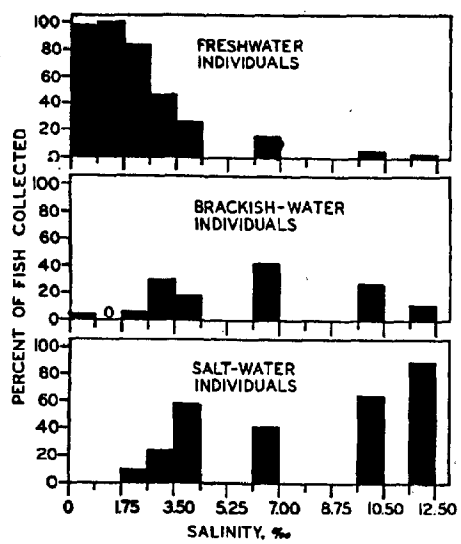


Fig. 6B. Freshwater, brackish water, and salt water fish sampled at various salinities in the lower Neuse River basin, N.C. Means based on salinity increments of 0.875 °/oo (Keup and Bayless, 1964).

present as did Herman et al. (1968) in a similar oligohaline environment. Harpacticoid copepods were very common in his samples at night, but in extremely variable numbers. They were virtually absent from samples taken during daylight hours. In one instance the average concentration (samples were taken vertically at 1 m intervals) was over 18,000 individuals/m^3 or about twice the maximum holoplanktonic concentration observed. He found that some of the variability could be explained by wind speed. Harpacticoid abundance in the water column was positively associated with surface wind velocity. Peters suggests that the harpacticoid copepods are positively rheotactic and respond to the wind induced turbulence, although light appears to be the main factor for the entrance and exit from the plankton community.

Ctenophores are also abundant and dominate the plankton at times. In a study in progress, R. J. Miller (personal communication) has demonstrated that there is an apparent seasonal bimodal cycle of abundance with peaks during April and September in 1967 and in June and November in 1968. In a study of ctenophore feeding rates in the Patuxent estuary, Bishop (1967) estimated that approximately 31% of the standing crop of Acartia tonsa was cropped by the ctenophores each day. Although ctenophores are apparently efficient and important carnivores, the fate of this consumed energy is unknown. Herman et al. (1968) cite two fishes, Peprilus alepidotus and Poronotus tricanthus which feed on adult ctenophores, but neither species in abundant in Pamlico River.

Keup and Bayless (1964) described the fish fauna in a similar estuary in North Carolina. They collectedfish by rotenone from 18 stations with a salinity range from 0 to 12 ppt, although only six of their stations were more saline than 4 ppt. They found 42 primarily fresh-water species and 20 salt-water or brackish-water forms. They did find a broad overlap of fresh and salt-water fish distributions with respect to salinity, however (Figure 6B). This supports the view that there is no sharp demarcation between oligohaline and mesohaline estuarine systems and that freshwater fish can and frequently do enter water with a salinity of 10 ppt or greater (approaching isosmotic conditions) and salt-water fish are commonly found in very low salinity water during the summer. In the Pamlico River, fish were sampled by otter trawl at several stations at monthly intervals during the spring, summer and winter of 1965. Samples taken in water of salinity between 3 and 10 ppt were composed substantially of salt-water species although the method of sampling was probably responsible for the virtual absence of fresh-water species in the collections. Twenty species in addition to the salt and brackish-water forms mentioned by Keup and Bayless (1964) were collected. Most of these were species which only stray into the estuary during the summer months. Two of the most unusual records were of a remora (Remora remora) caught by hook and line in 1966 near Indian Island, and a smooth dogfish (Mustelus canis) caught in a gill net in South Creek in 1965 in salinity estimated to be approximately 5 ppt. From our sampling, the dominant fish inhabiting the major oligohaline portion of Pamlico River are primarily salt-water species. The permanent and semi-permanent species are given in Table 4.

Table 4. Permanent and semi-permanent salt-water species inhabiting the oligohaline system (5-10 ppt) of Pamlico River, N. C.

Permanent Residents	
Common Name	Scientific Name
Common mummichog	*Fundulus heterocletus*
Rainwater killifish	*Lucania parva*
Naked goby	*Gobiosoma bosci*
White perch	*Roccus americanus*
Striped anchovy	*Anchoa epcetus*
American eel	*Anguilla rostrata*
Hogchoker	*Trinectes maculatus*

Present Year-round Except During Winter	
Common Name	Scientific Name
Tidewater silverside	*Menidia beryllina*
Rough silverside	*Membras vagrans*
Common silverside	*Menidia menidia*
Spot	*Leiostomus xanthurus*
Atlantic croaker	*Micropogon undulatus*
Pinfish	*Lagoden rhomboides*
Atlantic menhaden	*Brevoortia tyrannus*
Summer flounder	*Paralichthys dentatus*
Northern pipefish	*Sygnathus fuscus*

Migrating through System	
Common Name	Scientific Name
Hickory shad	*Alosa mediocris*
Alewife	*Alosa pseudoharengus*
Glut herring	*Alosa aestivalis*
American shad	*Alosa sapidissima*
Gizzard shad	*Dorosoma cepedianum*
Striped bass	*Roccus saxatilis*
Common sturgeon	*Acipenser oxyrhynchus*

Sacramento-San Joaquin Estuary, California

An extensive oligohaline zone exists in the estuary formed by the Sacramento and San Joaquin Rivers in California (Figure 7). The water flowing from the two rivers arrives at the Pacific Ocean through the Golden Gate, after passing through Suisun, San Pablo and San Francisco Bays.

Considerable information concerning the Sacramento-San Joaquin Estuary has been reported in two compilations of reports by the California Department of Fish and Game (Kelley 1966; Turner and Kelley 1966). Summarization of the data reported in those two documents will serve to describe the characteristics and structure of a west-coast oligohaline system.

Zonation of salinity and animals in the Sacramento-San Joaquin Estuary is shown in Figs. 8 A and B. As illustrated in Figure 8 A, the oligohaline system extends from the Delta into Suisun Bay. During late winter and early spring "floods", the zone may extend into Pablo Bay. In general, the estuary is "well-mixed" and the existance of a saline wedge is rare (Kelley 1966). During periods of flooding, however, a tongue of freshwater may extend through San Pablo Bay into San Francisco Bay.

An illustration of the organismal zonation is given in Figure 8B. Unfortunately, no data were available to describe the plant zonation in the area, but it is likely that grasses dominate the shallow, more oligohaline regions. Mya arenaria, the clam that is abundant in oligohaline regions on the upper west and east coasts of the United States, was found in significant numbers only in the mesohaline zone and seaward. Truly oligohaline species included the copepods Cyclops spp., Diaptomus spp. and Eurytermora affinis, with E. affinis being limited to the estuarine area. The most important zooplankter in the system was Neomysis awatschensis, the opossum shrimp which was characteristic of the oligohaline system. The Asiatic clam, Corbicula fluminea, was very abundant in the upper oligohaline area and sometimes formed dense beds. The mud clam, Macoma inconspicua, was characteristic in Suisun Bay and seaward; which matches its counterpart, Macoma baltica, in east coast estuaries. Two worms, Neanthes succinea and Polydora uncata, were characteristic benthos. Migrating through the system were the American shad, king salmon and striped bass.

The abundance and location of total net zooplankton throughout the Sacramento-San Joaquin Estuary are illustrated in Figure 9. Concentration ranged from less than 10,000 to more than 500,000 zooplankton per cubic meter. Concentrations were lowest during winter and highest during spring and autumn, with the peak populations occurring just seaward of the oligohaline zone.

Two species of Copepoda, Acartia clausi and Eurytemora affinis, and the mysid shrimp, Neomysis awatschensis, make up the bulk of the adult zooplankton (Painter 1966a). Acartia clausi, probably more indicative of the mesohaline (middle salinity plankton system), were much less abundant

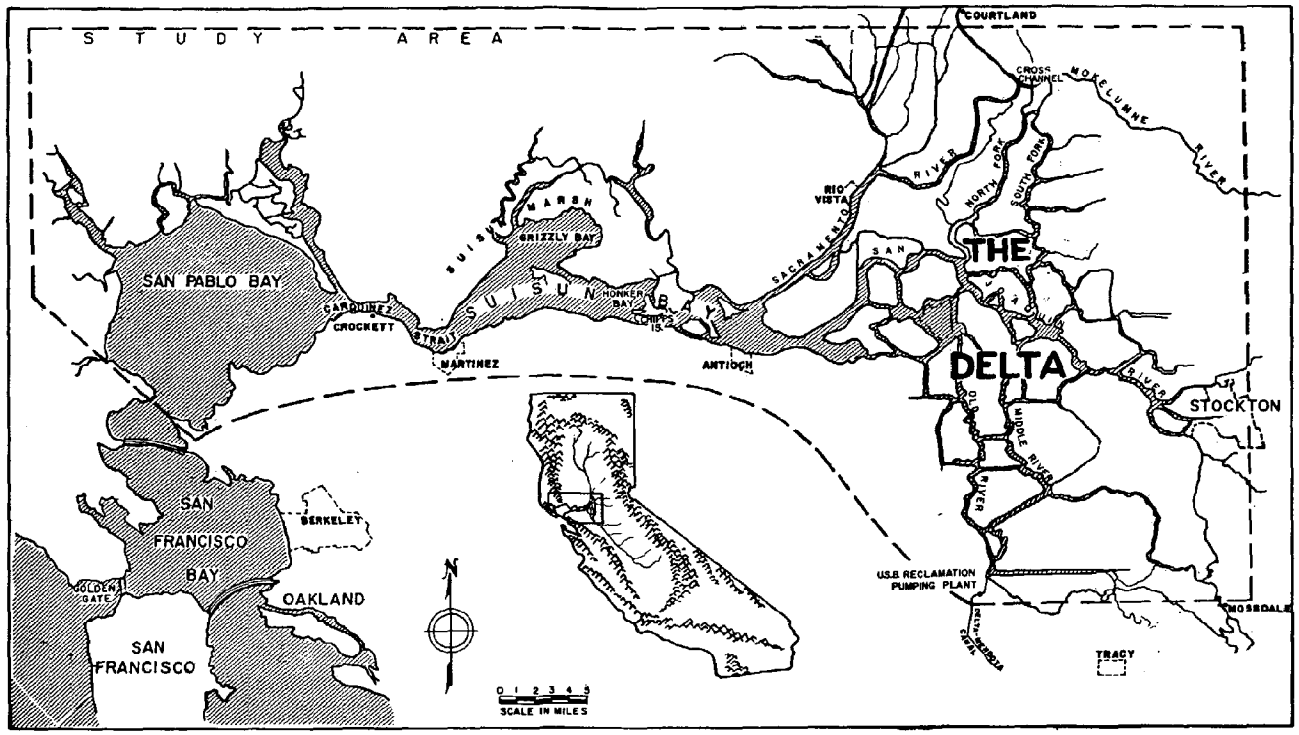


Figure 7. Map of the Sacramento-San Joaquin Estuary (From **Kelley 1966**; Fig. 1).

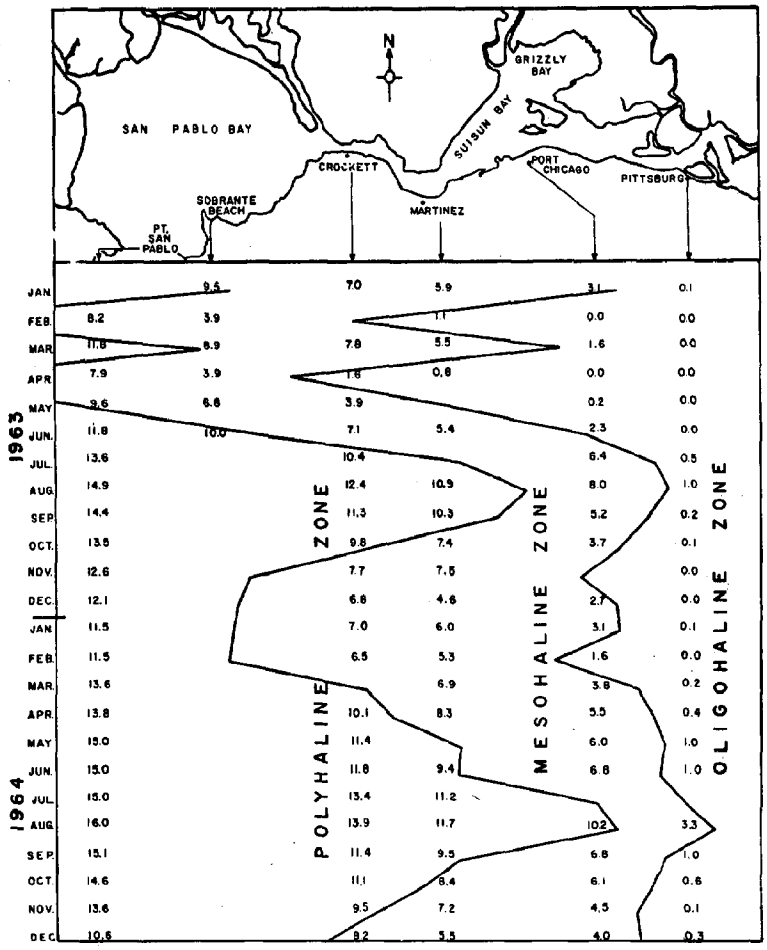


Figure 8A. Salinity changes during 1963-1964, showing the limit of the oligohaline zone. Figures are ppt chlorides (From **Kelley 1966; Fig.2**).

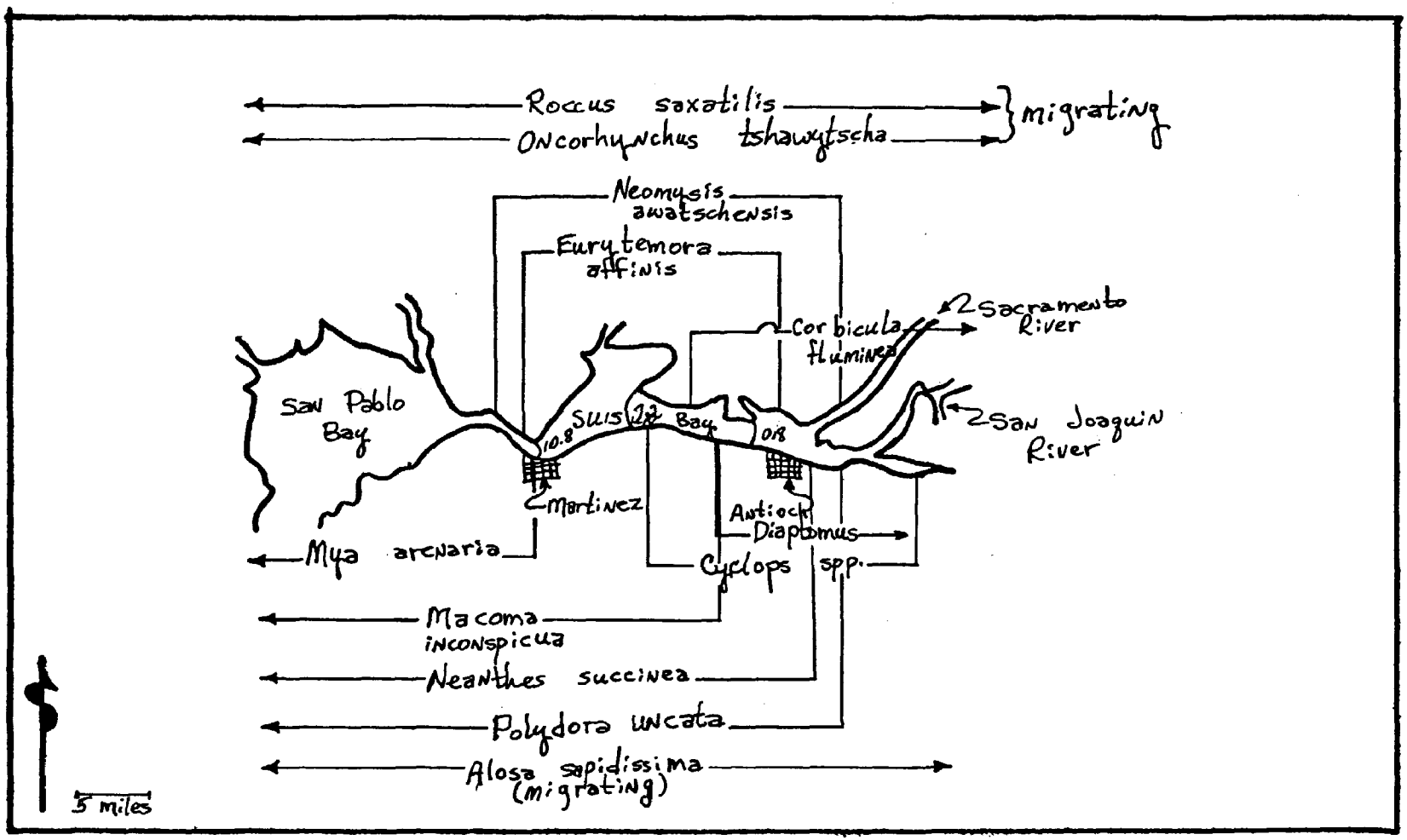


Figure 8b. Composite sketch of major components in the oligohaline zone of the Sacramento-San Joaquin Estuary and the limits of their distribution. Average salinity limits designated in parts per thousand. (From Painter 1966a, 1966b; Ganssle 1966).

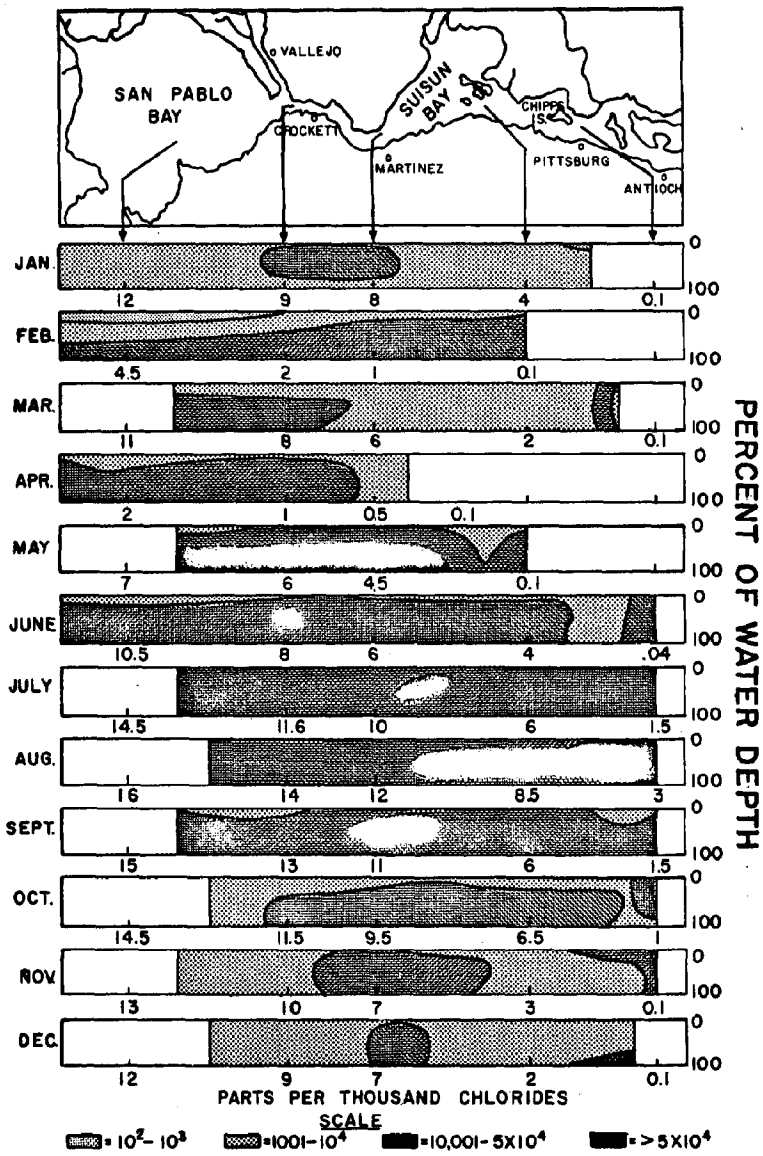


Figure 9. Seasonal changes in the distribution and abundance of total net zooplankton in the main channel of the estuary. Depth is shown as percent of the total depth of the channel. (From Painter 1966a; Fig. 2)

in the lower salinity areas (oligohaline system). E. affinis, apparently indicative of the oligohaline system on the lower west coast, were extremely abundant in the Suisun Bay and toward freshwater (Fig. 10). They were found in significant numbers in San Pablo Bay only during times that large freshwater contributions pushed the lower salinity plankton system seaward into the lower bay areas (cf. February, April and May 1963). Ganssle (1966) reported that E. affinis were important food organisms for the migrating young of the American shad and striped bass.

Several species of Cyclops, a cyclopoid copepod, were lumped by Painter (1966a) as Cyclops spp. Their distribution and abundance are shown in Figure 11. Cyclops spp. are generally thought to be limited to freshwater, but are commonly found in oligohaline systems and may be said to be characteristically present (Painter 1966a). During extensive flooding, the Cyclops were found to be present in the characteristically middle salinity San Pablo Bay (cf. February and April 1963). At least three species of Diaptomus, another oligohaline copepod, were found in the Sacramento-San Joaquin Estuary oligohaline system during most of the annual cycle (Painter 1966a). They, however, were never collected in San Pablo Bay, even during extensive flooding.

The oppossum shrimp, Neomysis awatschensis, is the most important food organism in the diet of young-of-the-year fish in the Sacramento-San Joaquin Estuary (Ganssle 1966). The distribution and abundance of this mysid in the Sacramento-San Joaquin oligohaline system is shown in Figure 12. The distribution is characteristically oligohaline and extended beyond this zone only during extensive flooding. Indeed, the largest populations occurred nearer the freshwater end of Suisun Bay.

The distribution of zoobenthos is important in characterizing oligohaline systems. The distribution of the clam, Rangia cuneata, is an important indicator of oligohaline systems in the Atlantic and Gulf coasts (compare the Pamlico River Estuary and the data presented by Odum 1967b for the Texas coast). Rangia cuneata, however, are not found in the Sacramento-San Joaquin Estuary (Painter 1966b). Mya arenaria, usually characteristic of mesohaline areas of the Atlantic and Gulf coasts, are present in the San Pablo Bay, California and are generally seaward of the oligohaline system (Figure 8B).

The amphipod, Corophium, distribution indicates characteristic speciation according to the salinity of the system (Figure 13). C. acherusicum was collected in the middle salinity system and in some cases occurred in high concentrations. It was present in Suisun Bay only during autumn when the salinity of the system was relatively high (above 10 ppt). However, C. stimpsoni and C. spinicorne were characteristically oligohaline. As shown in Figure 13, very low concentrations of all three species occurred in the area of salinity overlap (i. e., the zone of highly fluctuating salinity with season). These amphipods are important as food organisms for young striped bass, a migrating subsystem in the Sacramento-San Joaquin Estuary (Ganssle 1966).

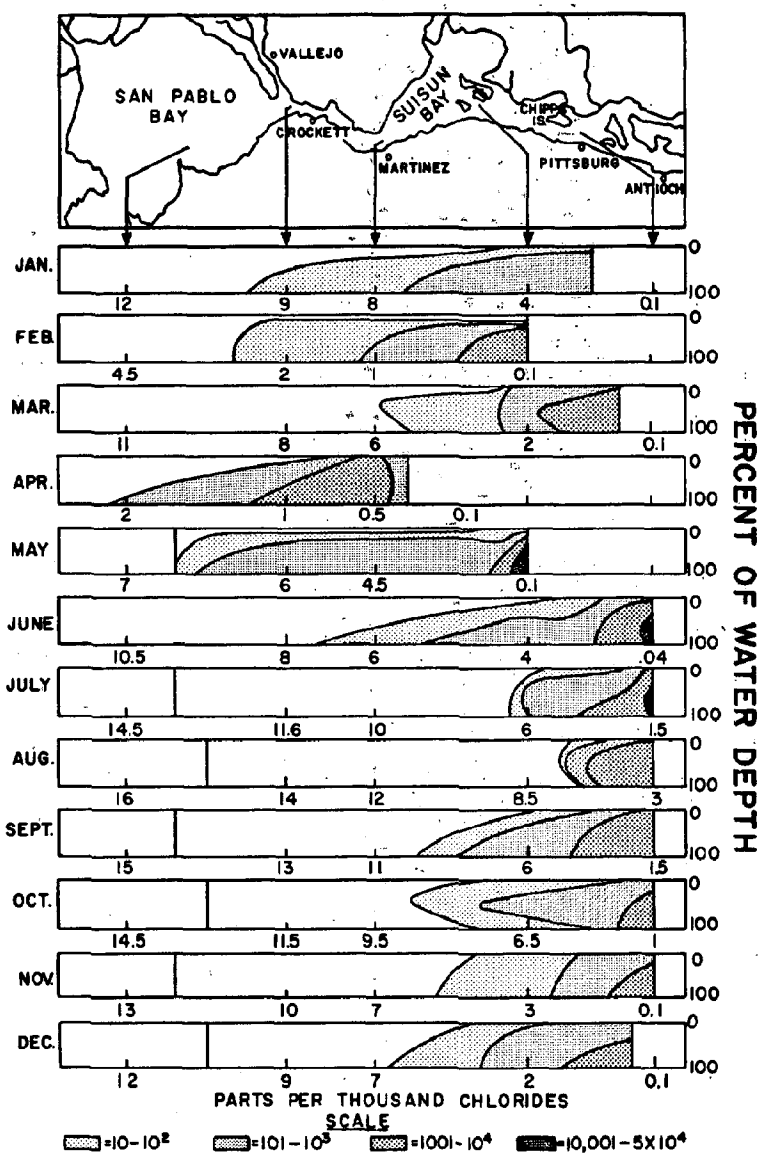


Figure 10. Seasonal changes in the distribution and abundance of Eurytemora affinis in the main channel of the estuary. Depth is shown as percent of the total depth of the channel. (From Painter 1966a; Fig. 5)

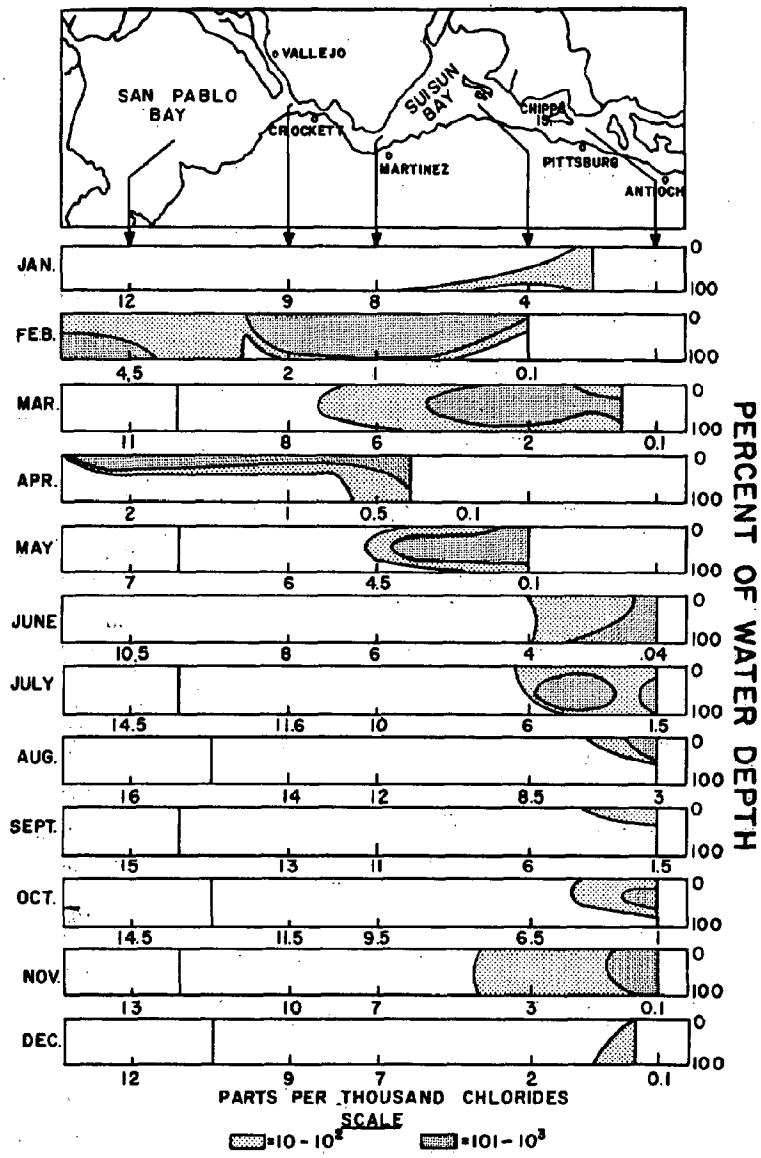


Figure 11. Seasonal changes in the distribution and abundance of Cyclops spp. in the main channel of the estuary. Depth is shown as percent of the total depth of the channel. (From Painter 1966a; Fig. 9)

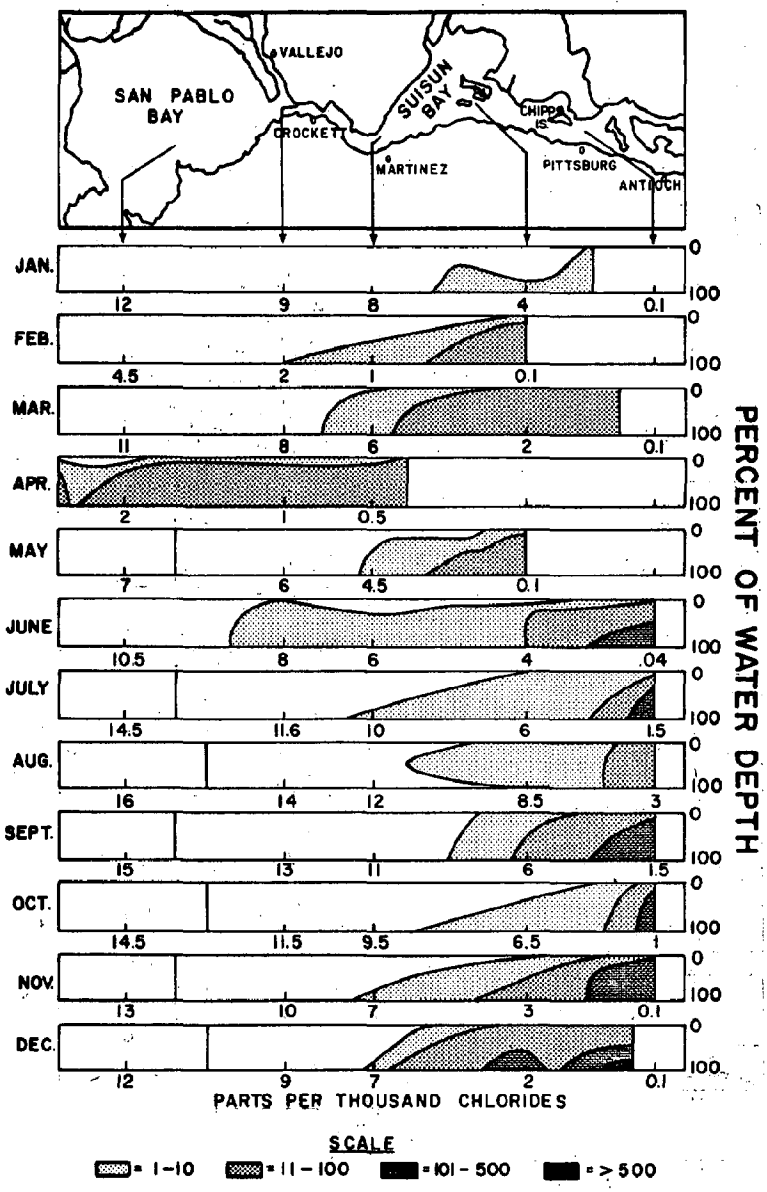


Figure 12. Seasonal changes in the distribution and abundance of Diaptomus spp. in the main channel of the estuary. Depth is shown as percent of the total depth of the channel. (From Painter 1966a; Figure 7).

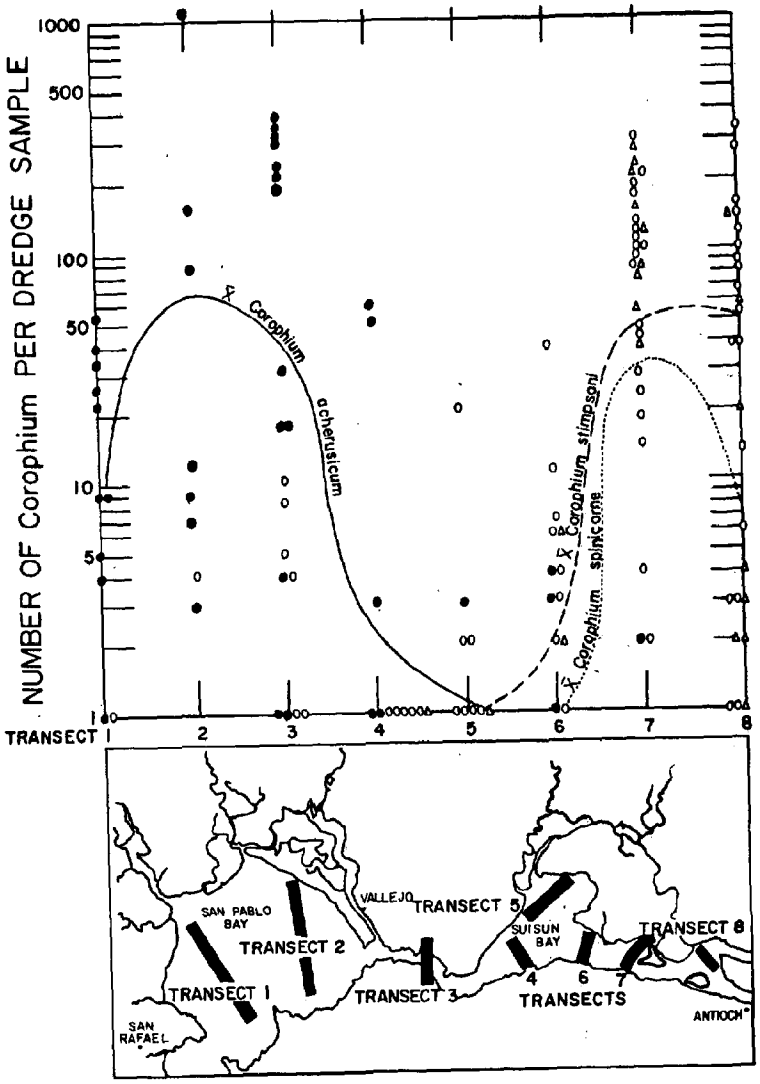


Figure 13. Distribution of three species of Corophium through the reach of changing salinity. Plotted points represent the numbers in individual Peterson dredge samples collected from the transects shown on the map. Open circles represent C. stimpsoni; open triangles, C. spinicorne; and blackened circles, C. atcherusicum. The curves represent the means of all (281) samples collected on each transect during July-September 1963. (From Hazel and Kelley 1966 ; Fig. 1)

Painter (1966b) reported a large difference in the total biomass of benthic animals in the estuary (Fig. 14). Mollusca were characteristic of the seaward end of the estuary, while annelids were prominent at the fresher end. Within the zone of salinity fluctuation, the biomass and diversity of organisms were low.

Of the 60 species of fishes collected in the Sacramento-San Joaquin Estuary, 36 were typically saltwater forms and were generally restricted to the San Pablo Bay area (Ganssle 1966). The more abundant fishes in the oligohaline system were anadromous and composed a large migrating subsystem. Generally, the migrating forms migrated through the oligohaline system during times of maximum food availability (see chapter on Migrating Subsystems for discussion). Pacific herring, American shad, striped bass and the king salmon represent the most abundant members of the migrating subsystem through the Sacramento-San Joaquin Estuary oligohaline system (Ganssle 1966).

The monthly catch of young-of-the-year Pacific herring, Clupea pallasi, is shown in Figure 15. Large numbers of the young appear in the oligohaline system during spring.

Adult American shad migrate from the sea into streams to spawn, thus passing through the oligohaline system as adults. As shown in Figure 16, young-of-the-year shad appear in the Sacramento-San Joaquin oligohaline system during the autumn. Ganssle (1966) reported that stomach examination of young shad revealed that the major food item was Neomysis awatschensis, abundant during the same season in the Sacramento-San Joaquin oligohaline system.

The king salmon migration through the Sacramento-San Joaquin Estuary is reportedly the largest on the Pacific coast (Ganssle 1966). The migration of adult salmon upstream occurs mainly during autumn, with spawning taking place far upstream. Young salmon move downstream and into the estuary during February to April, arriving during maximum food availability. The most abundant food organism in the stomachs of young salmon was Neomysis awatschensis, characteristically oligohaline.

Striped bass adults move into the Sacramento-San Joaquin system during autumn, where they spend the winter (Ganssle 1966). During spring they move further upstream where spawning takes place. The spent adults usually move through the estuary back to the sea by summer. The young-of-the-year then enter the estuarine area during late summer and autumn (Figure 17). Neomysis awatschensis made up a major portion of the diet of this fish in the oligohaline system, although amphipods (Corophium sp.) were significant.

Baltic Sea, U. S. S. R.

Representative of north temperate oligohaline systems is the Baltic, located in Russia (Figure 18). Zenkevitch (1963) devotes a long chapter to the description and explanation of the system characteristics of this rather deep yet distinctively oligohaline system. Due to the lack of comprehensive

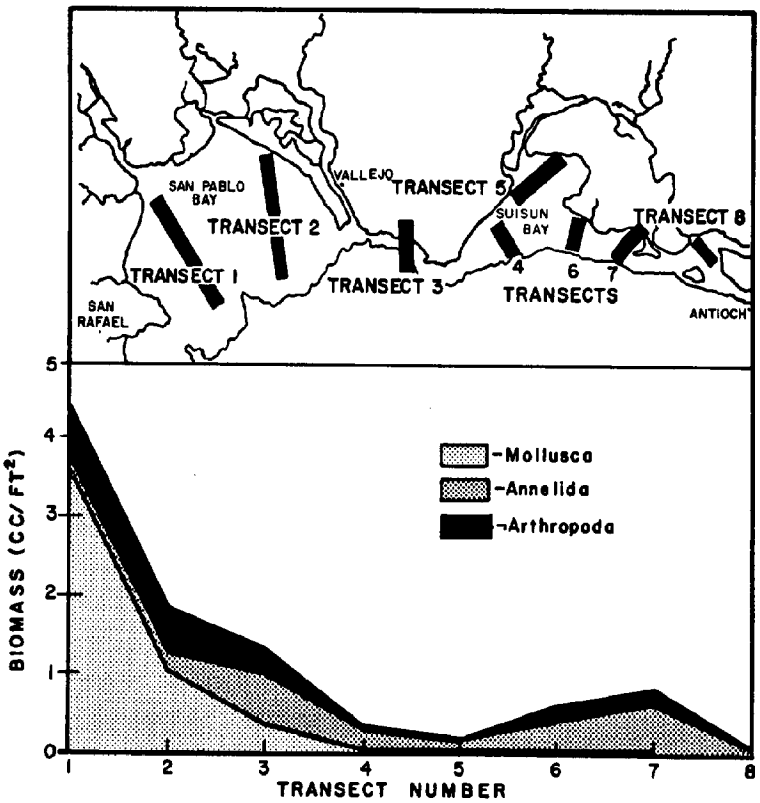


Figure 14. Average monthly biomass of fish and wildlife food organisms from eight transects in San Pablo and Suisun Bays. (From Painter 1966b; Fig. 4)

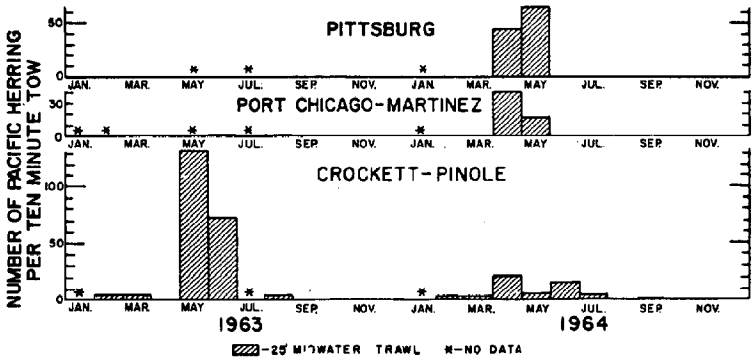


Figure 15. Monthly trawl catch of young-of-the-year Pacific herring, Clupea pallasi. (From Ganssle 1966; Fig. 4)

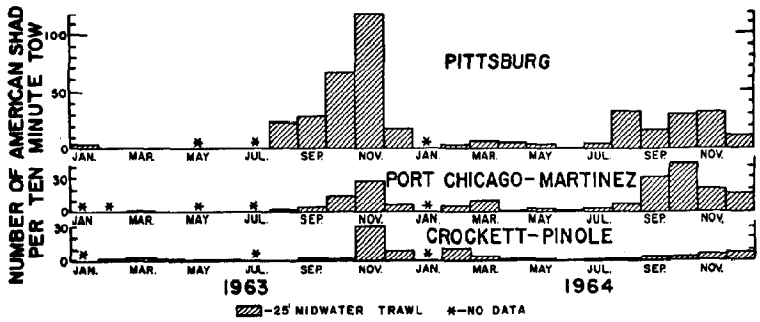


Figure 16. Monthly trawl catch of young-of-the-year American shad, Alosa sapidissima. (From Ganssle 1966; Fig. 3)

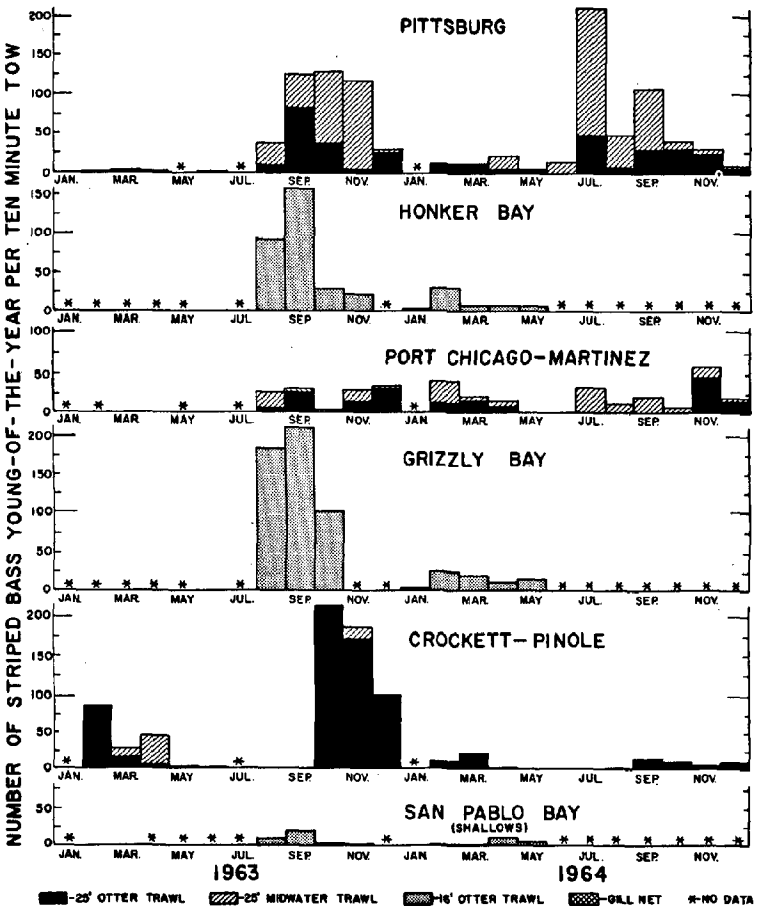


Figure 17. Monthly trawl catch of young-of-the-year striped bass, Roccus saxatilis. (From Ganssle 1966; Fig. 10)

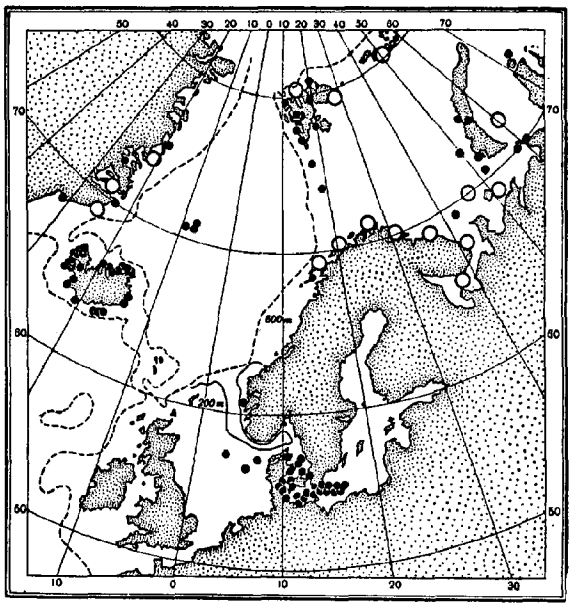


Figure 18. Location of the Baltic Sea (From Zenkevitch 1963; Figure 166).

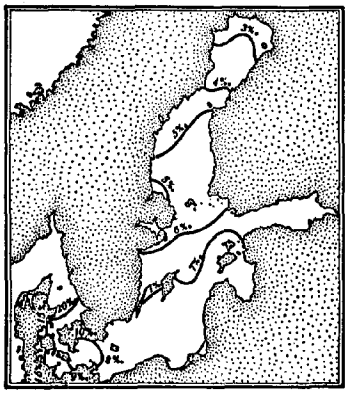


Figure 19. Surface salinity of the Baltic Sea (From Zenkevitch 1963; Fig. 136).

studies of American north temperate oligohaline systems, we shall describe the Baltic from Zenkevitch's treatise as an example. The Gulfs of Bothnia (northwest) and Finland (northeast) of the Baltic represent oligohaline systems.

As shown by the salinity profiles in Figure 19, almost all of the Baltic Sea lies within the oligohaline zone, especially the northwestern arm. Due to the tidal flux and winds, along with the inflow of considerable freshwater, the salinity fluctuates and is strongly stratified. Saline water moves from the North Sea underneath the freshwater layer from the northern arms of the Baltic.

The zonal distribution of fauna in the Baltic Sea is illustrated in Figure 20. Zenkevitch explains that in the outer oligohaline zone one finds a community that is diversified and rich in biomass, but as one moves to the east and north to the headlands almost pure populations of Macoma baltica are present. These large populations of Macoma baltica are comparable to the findings in oligohaline zones in temperate estuaries of the United States. Also found in the oligohaline system of the Baltic are amphipods, Pontoporieia sp., and the worm Nereis diversicolor. Moving through the system, as migrating subsystems, are the large populations of herring and cod. Just as in other oligohaline systems, benthic forms make a large proportion of the fauna.

Important in the plant populations of the upper Baltic are the bottom plants (Zenkevitch 1963). Their distribution, however, is governed by the distribution of salinity (Figure 21). Although, there is an impoverishment of the flora as one goes further up the Baltic, this impoverishment is not as distinct as that of the fauna (i. e., several species of plants are able to survive in contrast to a very few species of animals). Prominent among the attached plants in the oligohaline system are Najas marina, Myriophyllum spicatum and three species of Potamogeton, similar to attached plant populations in sourthern temperate oligohaline systems. Ruppia maritima and Scirpus tabernaemontani are sometimes prominent, especially in the lower reaches of the oligohaline system.

The penetration of marine and brackish water plants into the Baltic is illustrated in Figure 22. In spite of the low salinities commonly found in the upper Baltic, the occurrence of several species of plants in the oligohaline zone is common.

The fauna of the North Sea, which is undoubtedly the source of the marine and euryhaline fauna available to the Baltic Sea, totals about 1500 species (Zenkevitch 1963). There is a steady decrease in the number of species as one proceeds from the North Sea to the upper reaches of the Baltic Sea, until at the oligohaline zone only 55 species persist (Zenkevitch 1963, Table 126). The penetration of fauna from the North Sea into the Baltic upper reaches is illustrated in Figure 23. It is notable that the main species of zoobenthos in the oligohaline zone are Macoma sp., Neomysis sp. and Nereis sp., very similar to the speciation in the oligohaline zones of more

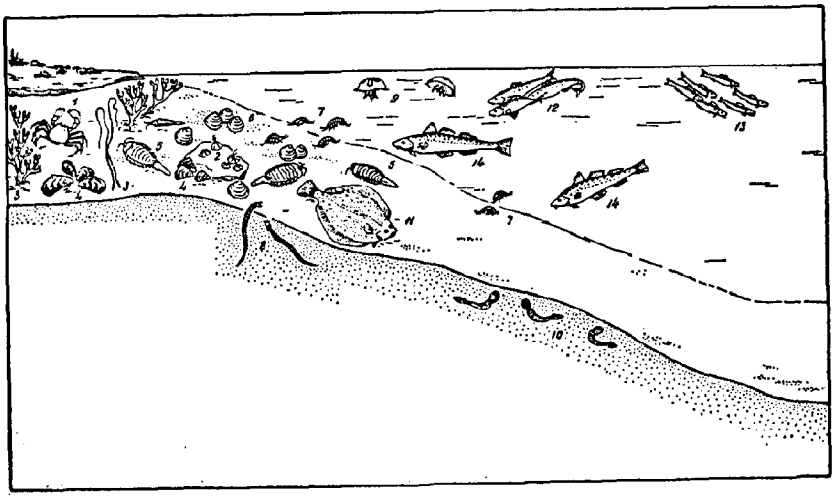


Figure 20. Zonal distribution of Baltic fauna: 1) Eriocheir sinensis; 2) Balanus improvisus; 3) Fucus vesiculosus and Chorda filum; 4) Mytilus edulis; 5) Mesidothea entomon; 6) Macoma baltica; 7) Pontoporeia affinis and P. femorata; 8) Nereis diversicolor; 9) Aurelia aurita; 10) Priapulus caudatus; 11) Pleuronectes flesus; 12) Herring; 13) Sprattus sprattus balticus; 14) Cod. (From Zenkevitch 1963; Fig. 161).

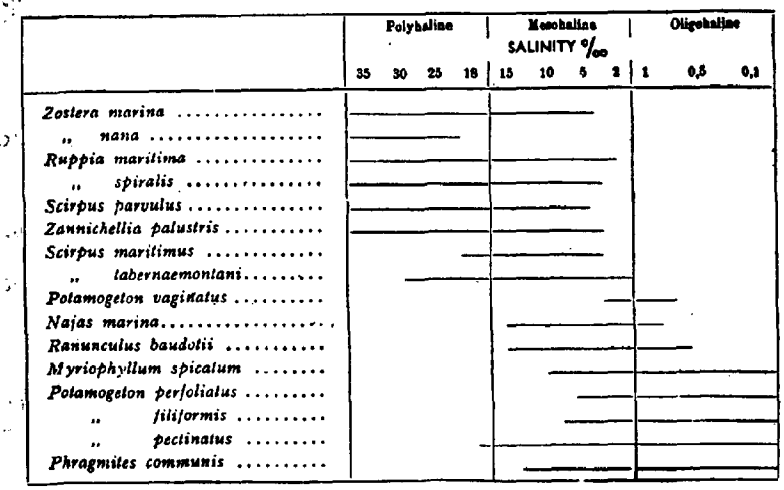


Figure 21. Correlation between salinity and the distribution of flowering marine plants (From Zenkevitch 1963; Fig. 144b).

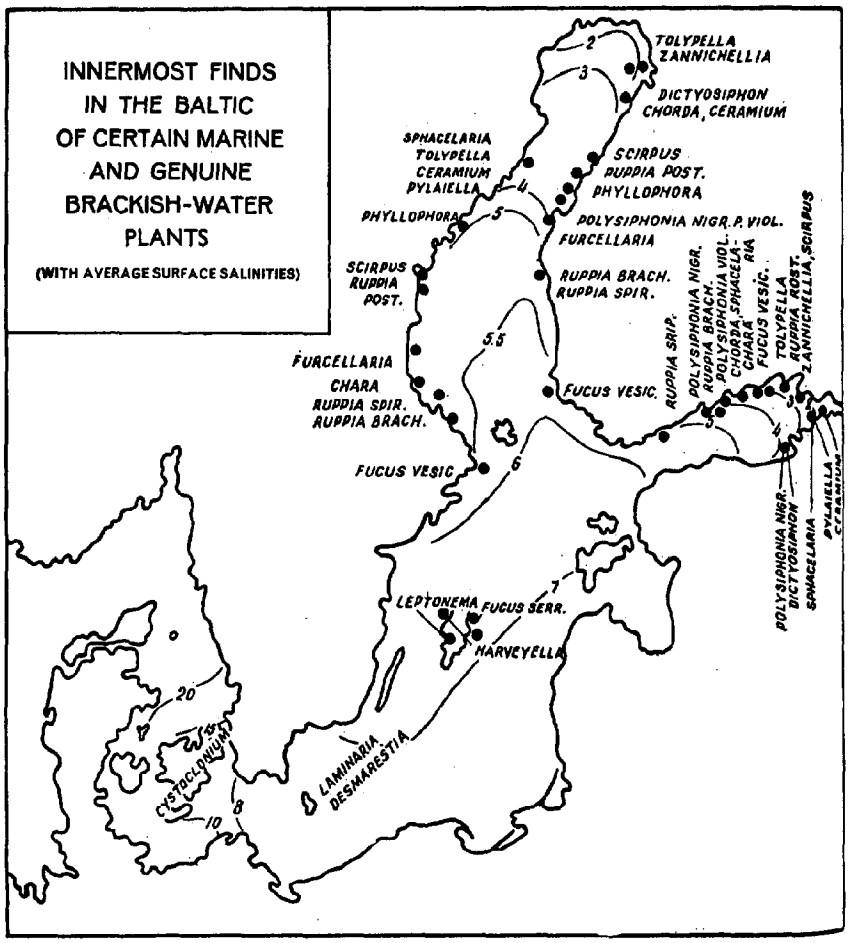


Figure 22. Penetration of some marine and brackish-water plants far into the Baltic Sea (From Zenkevitch 1963; Fig. 144A).

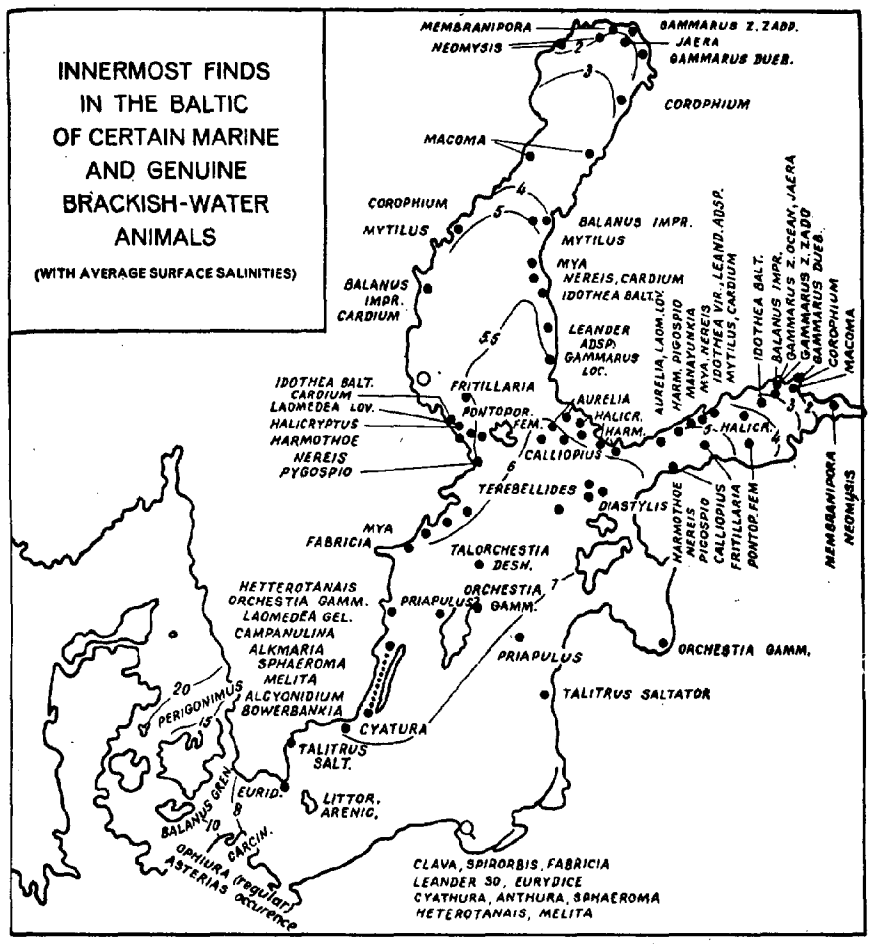


Figure 23. Penetration of some marine and brackish-water animals far into the Baltic Sea (From Zenkevitch 1963; Fig. 146).

southern temperate estuaries. Corophium sp., also present in the oligohaline zone of the Sacramento-San Joaquin Estuary, California (Hazel and Kelly 1966), are relatively common in the upper Baltic.

The distribution of main bottom communities is given in Figure 24 (the numbers indicate biomass in gm/m^2). The quantitative biocoenotic distribution of the bottom fauna of the Baltic Sea presents a fairly simple picture in consequence of the qualitative impoverishment of the population and an important factor of environment--salinity decrease from west to east. The biocoenosis of the Gulf of Finland is the Macoma balthica community and that of the Gulf of Bothnia is M. balthica in the shallow southern portion and Pontoporeia affinis-Mesidothea in the upper regions and in the deeper southern portion. It is important to note that the average biomass of the zoobenthos decreases considerably as one enters the oligohaline zone.

Plankton distribution in the Baltic follows a qualitative change as one leaves the North Sea and continues through the Baltic Sea (Zenkevitch 1963). Prominent among the phytoplankton in the Gulfs of Finland and Bothnia is Chaetoceros danicus and the ciliates Helicostomella and Aphanizomenon. The zooplankton of the oligohaline system are represented mainly by the copepods Eurytemora hirundoides, E. affinis, E. hirundo, Acartia bifilosa in some cases mostly by A. tonsa and Limnocalanus grimaldi (Figure 25). Blooms of diatoms occur during the spring and autumn with the inflow of large amounts of freshwater, which in turn support large populations of zooplankton.

The decrease in numbers of animal species with salinity decrease is illustrated in Figure 26. Although the diversity of organisms is relatively low in the oligohaline systems of the Gulfs of Finland and Bothnia, the number of individuals of each species is quite large.

Important migrating fishes in the oligohaline system include the Baltic herring (Culpea harengus), sprat (Sprattus sprattus), and cod (G. morrhua). All of these fishes are plankton or zoobenthos consumers, and as such form the terminus of the abbreviated food-chain in the oligohaline system of the Baltic Sea.

Lake Pontchartrain, Louisiana

Back of New Orleans is an oligohaline estuary, Lake Pontchartrain and Lake Borgne, Louisiana (Fig.27) in which Darnell (1958;1961) Fairbanks (1963) and others have studied food relations as shown in Figs. 28-32. Many of the food chains (Fig. 28) were traced to organic detritus pool which came in part from outside sources in marshes (Fig. 27) supplemented by phytoplankton (Fig. 29). In years when floods of the Mississippi threaten New Orleans, waters are bypassed through the Bonne Carre spillway through the lake with a flushout. The alternation of flushing freshwaters and interflood salt water regimes is characteristic of many natural bayous of the Louisiana delta region. One dominant bottom animal is the Rangia clam (Fig. 30) which grows dwarf populations in vast numbers that are used to pave the roads in the way that oyster shells are used in many other states. A general diagram of benthic organisms in Lake Pontchartrain-Lake Borgne is given in Figure 31. Growth rate for Rangia in similar waters in North Carolina is given by Wolfe and Petteway (Fig. 32).

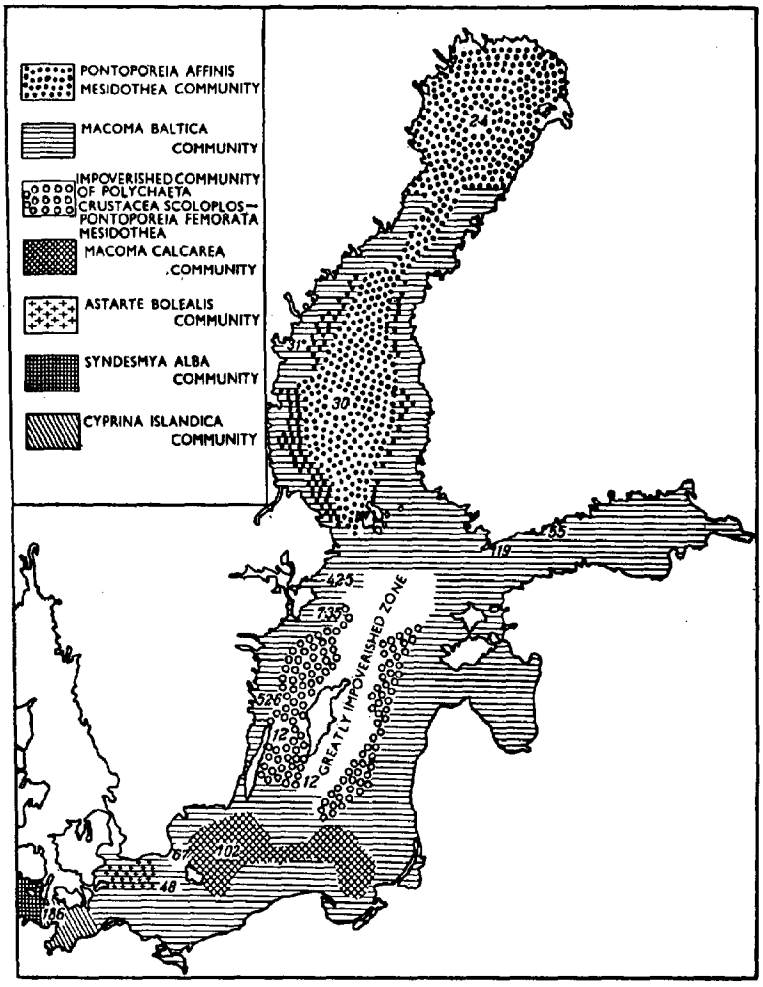


Figure 24. Distribution of bottom communities in the Baltic Sea (From Zenkevitch 1963; Fig. 149).

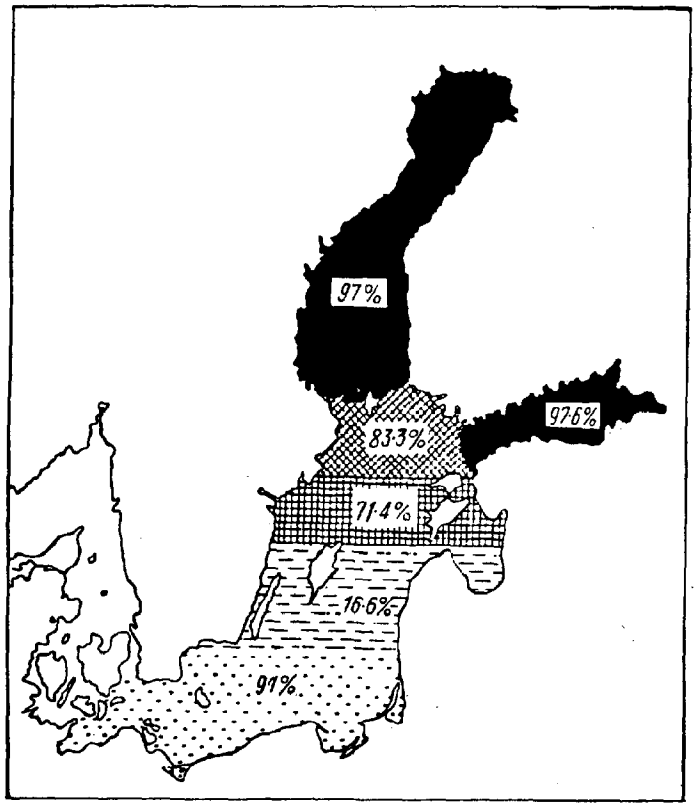


Figure 25. Distribution of the copepods Limnocalanus grimaldi in the Baltic Sea (From Zenkevitch 1963; Fig. 162A).

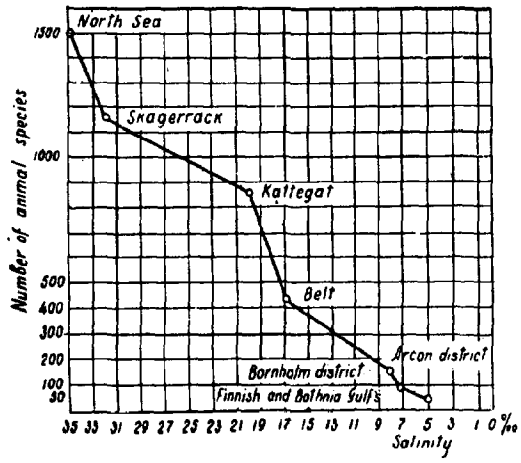


Figure 26. Decrease in number of species from North Sea to Baltic compared with the decrease in salinity (From Zenkevitch 1963; Fig. 145C).

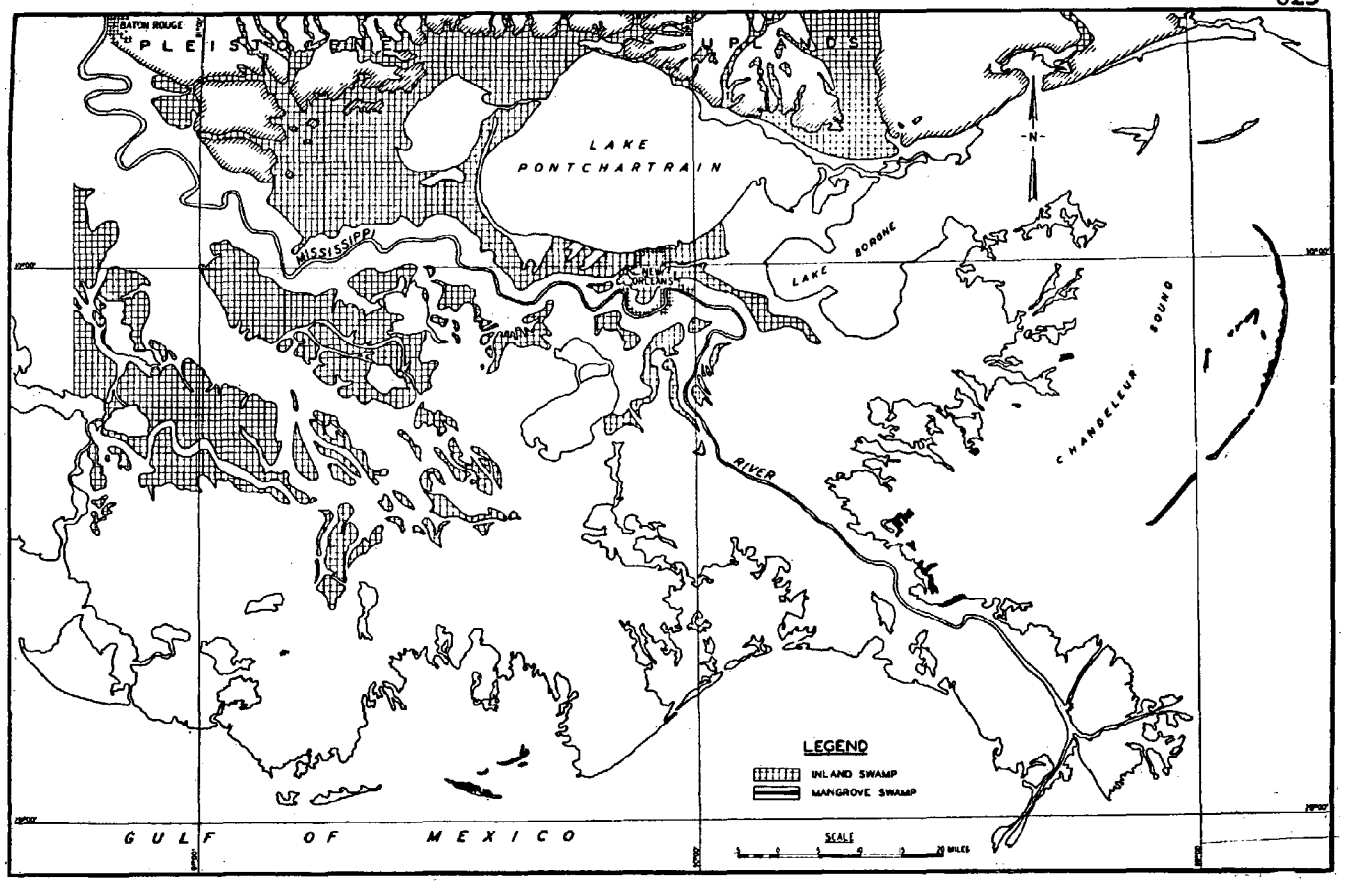
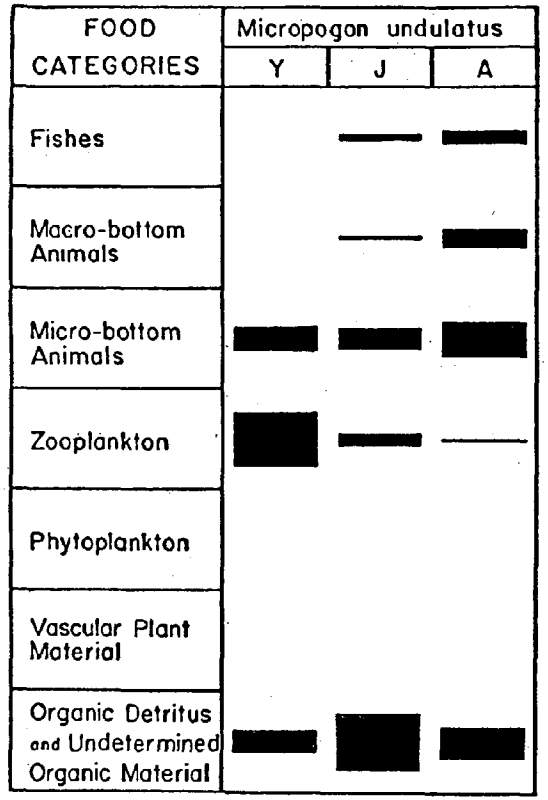
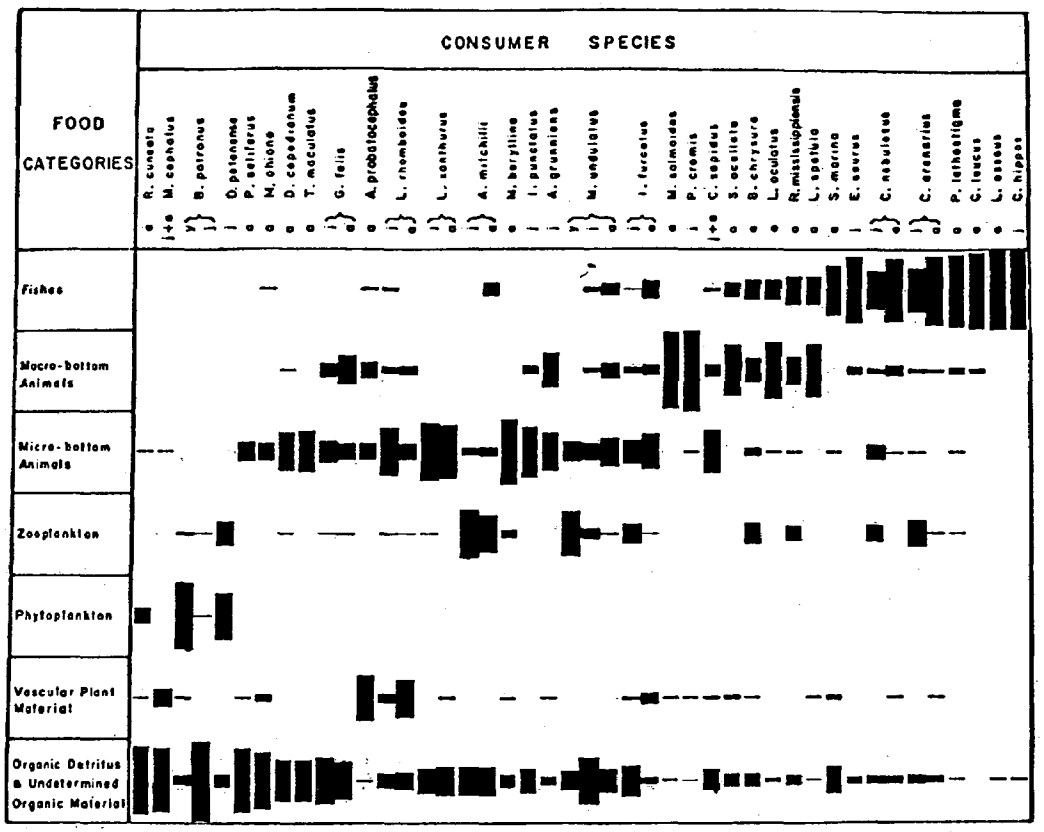


Fig. 27. Lake Pontchartrain (oligohaline estuary) surrounded by swamp drainage (Kolb and van Lopik, 1966).

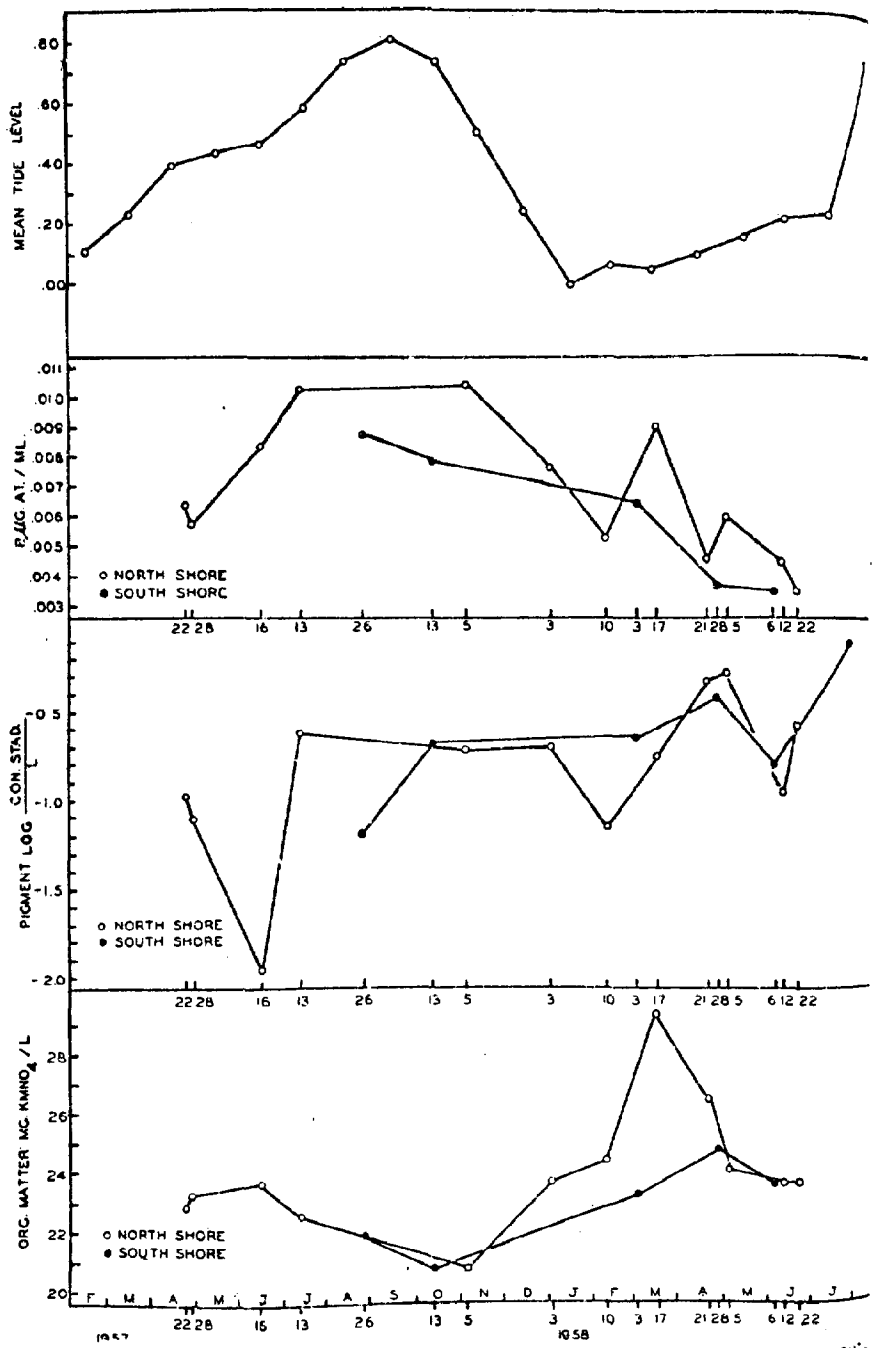


Trophic spectra for young, juvenile, and adult stages of the Atlantic croaker (*Micropogon undulatus*) from Lake Pontchartrain. Note the shift in emphasis from zooplankton in the young through detritus in the juvenile to bottom animals and fishes in the adult.



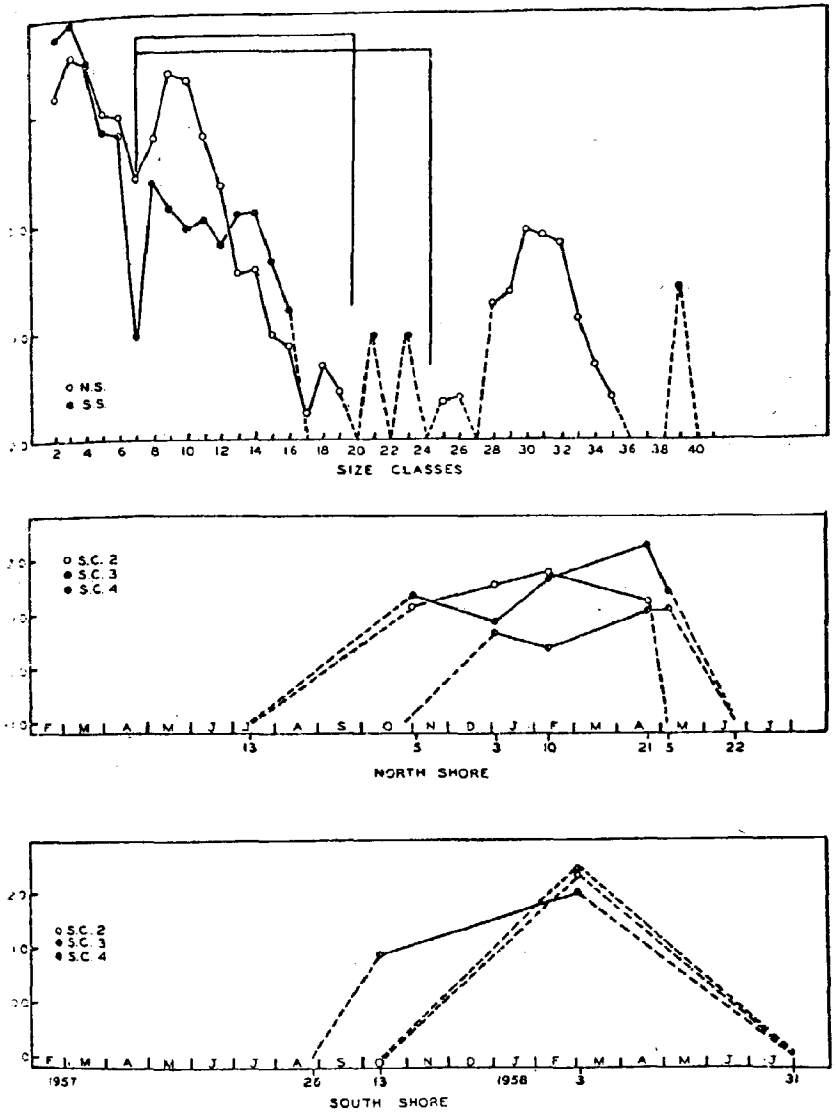
Trophic spectra for the most important consumer species of the Lake Pontchartrain community. Note relatively little utilization of phytoplankton, vascular plant material, or zooplankton, but heavy emphasis upon detritus, bottom animals, and fishes.

Fig. 28. Food relations in oligohaline waters of Lake Pontchartrain, Louisiana. (Darnell, 1961).

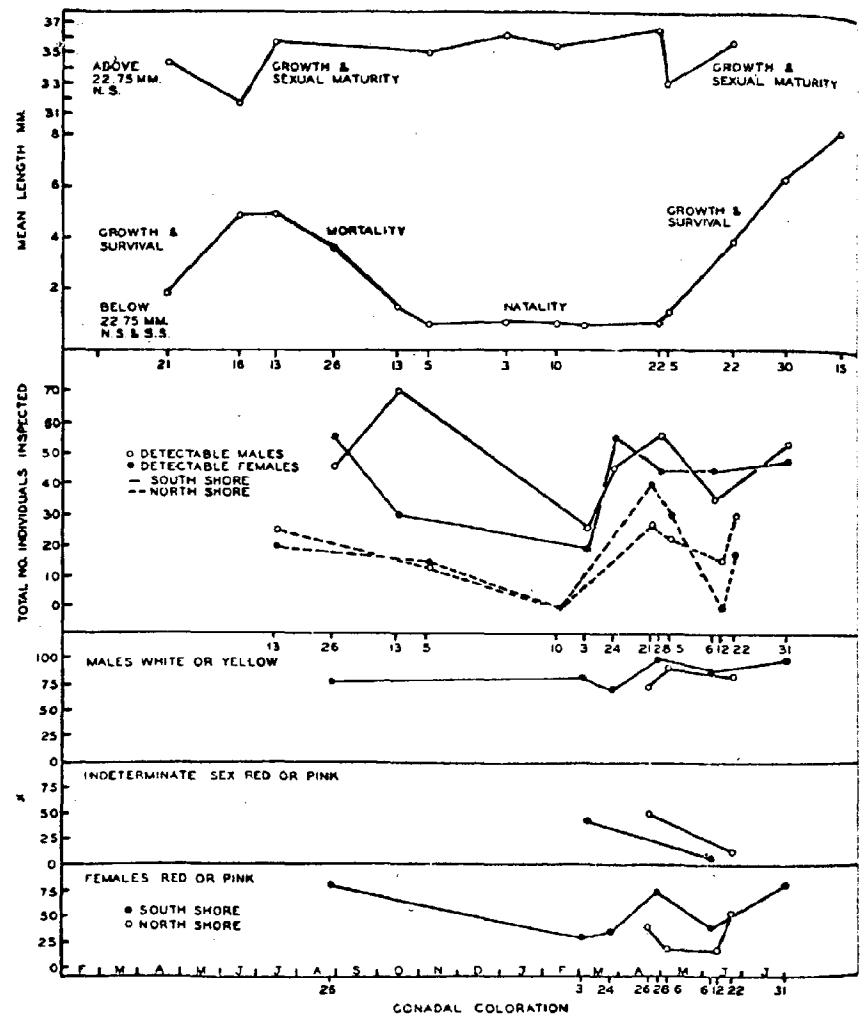


Figures 5-8. 5. (Top) Distributions of predicted monthly mean tide levels (1957-19[illegible]) for Long Point, Lake Borgne (in feet above mean low water). 6. (Second) Distributions of estimates of total phosphorus from within the lake only. 7. (Third) Distributions of phytoplankton pigment concentration from within the lake only. 8. (Bottom) Distributions of organic matter from within the lake only.

Fig. 29. Tides, nutrients, photosynthetic pigments, and organic matter in waters adjoining Lake Pontchartrain, La. (Fairbanks, 1963).

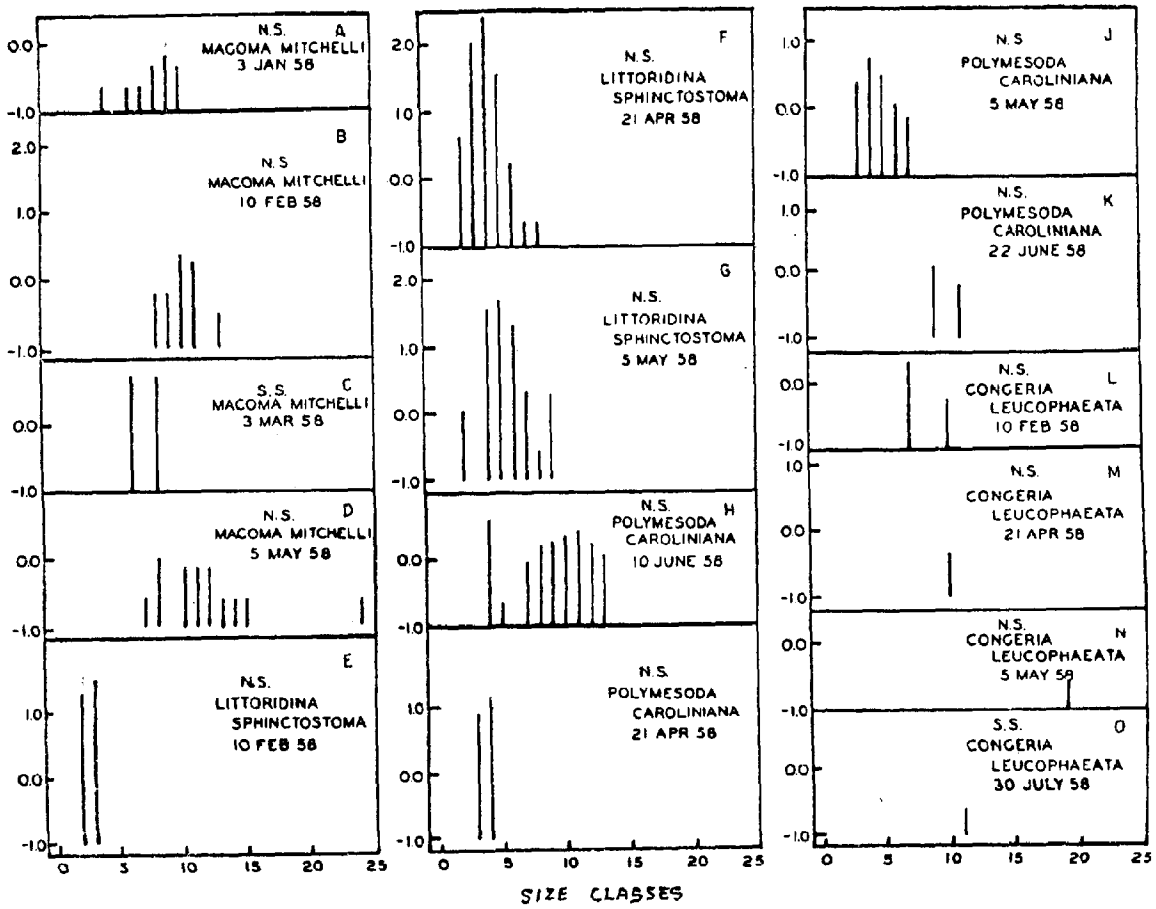


13. (Top) Distributions of mean density of size classes; dashed lines in- size classes having densities estimated to be no greater than the antilog of -2.0 sq. ft.), NS = north shore area, SS = south shore area; right angle lines delimit lasses involved in testing the density estimates of juveniles (see text). 14. (Middle) nal distributions of density of the three smallest size classes of the north shore area; d lines indicate dates for which densities were estimated to be no greater than the g of -1.0 (0.1/sq. ft.), SC = size class (see Table 2 for actual sizes). 15. (Bottom) nal distributions of density of the three smallest size classes of the south shore area ols as in fig. 14).



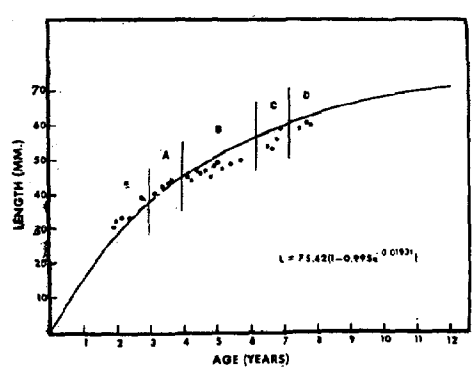
19. (Top) Distributions of seasonal mean length of north shore adu and of combined north and south shore juveniles; NS = north shore area, SS = sou shore area. 20. (Middle) Seasonal distributions of determinable sexes in the study area detectable = determinable. 21. (Bottom) Seasonal distributions of gonadal coloration ac cording to sex; indeterminate = non-determinable.

Fig. 30. Size distributions and seasonal characteristics of dominant Rangia clams in Lake Pontchartrain, La. (Fairbanks, 1963).



Distributions of population densities of associated molluscs; NS=north shore area, SS=south shore area (see Table 2 for actual sizes).

Fig. 31. Invertebrates in Lake Pontchartrain-Lake Borgne (Fairbanks, 1963)



Theoretical growth of *Rangia cuneata* Gray, expressed by von Bertalanffy growth curve with mean values of a and k (Table 1). Points are modal lengths of size groups A-E from Fig. 1, fitted to the curve as explained in the text.

Fig. 32. Growth of Rangia clams (Wolfe and Petteway, 1968).

DISCUSSION

The overwhelming characteristic of the oligohaline systems is the low salinity and great shocks of freshwater floods. Organisms capable of surviving the rigors of the system are few, but those that do, manage to flourish at certain seasons of the year. Important adaptations include attachment to avoid being swept away during high flow rates and the ability to withstand salinity variations.

Plants in the oligohaline regime include such freshwater forms as Najas and Potamogeton and the brackish water plant Ruppia maritima. It seems to make little difference whether the oligohaline system is located on the east or west coast, north or south, because the attached vegetation always appears to fall into those main categories. Benthic diatoms are common on the oligohaline mud flats and dinoflagellates dominate the phytoplankton.

Fauna include certain molluscan species that have special filtering ability to utilize the tremendous organic content of the muddy river water. Macoma balthica, for example, seems to be a common inhabitant of widely located oligohaline systems. Rangia cuneata is a common inhabitant of southern oligohaline zones, but is normally replaced by other clams in more northern areas. Nereis succinea, a polychaete, is common in the zoobenthos of all oligohaline systems except those of the more southern Gulf of Mexico coast.

Migrating subsystems are important constituents of the oligohaline system and channel much of the energy harvested by man. Common among these migrating forms are the herring-like plankton-feeding fishes represented by menhaden (Brevoortia patronus) on the Gulf of Mexico coast, shad (Alosa sapidissimus) and menhaden (Brevoortia tyrannus) on the Atlantic coast, shad (Alosa sapidissimus) and herring (Clupea pallasi) on the lower Pacific coast, and herring and cod in the Baltic Sea. Other migrating forms include carnivorous striped bass (Roccus saxatilis) on the east and west coasts of the United States.

In spite of the low diversity and biomass of organisms in the oligohaline systems, they are relatively highly productive due to the constant influx of organic fuels via rivers from the land.

Chapter C-9

MEDIUM SALINITY PLANKTON SYSTEMS

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INTRODUCTION

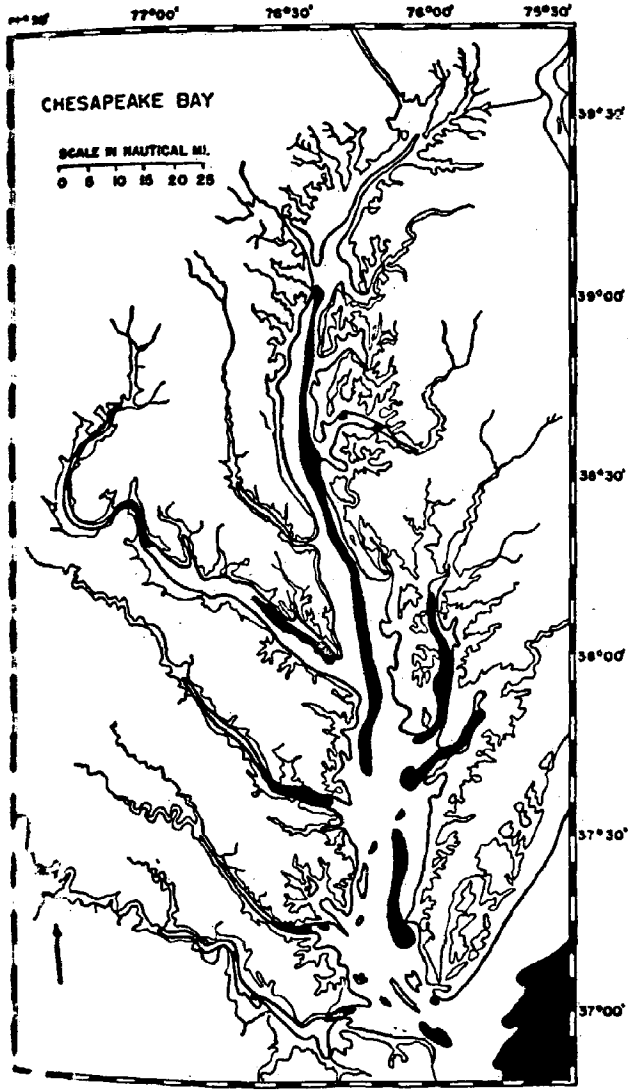
The continuum of overlapping biological forms along the course of an estuary is obvious to even the casual observer. In eastern North Carolina tree-edged rivers become broader and edged by grassy marsh as they approach the sea. Fishermen recognize such differences intuitively and respond by varying their choice of bait, site, and fishing technique. Estuarine biologists, geologists, and hydrologists also recognize gradations along the estuary. As with any system which in fact is a continuum, it is often convenient to describe and assign names to sub-systems selected for special consideration. One can then focus attention on a particular point in the continuum and then observe "flow" toward or away from it. The middle reach of an estuary possesses an assemblage of interrelated characteristics such that the concept of the "middle estuary" proves useful to those who study estuaries. Although the precise physical limits of this portion of an individual estuary will remain difficult to define and thus a source of controversy, a rather arbitrary working definition has been accepted by many. Characteristics of the middle estuary correspond most closely with portions of the estuary having average salinities between 5-18 ppt.

The middle estuary is important because the greatest area of many North American estuaries is of this type, and it is this portion which provides primary support for certain fisheries (e.g., blue crab and oyster). In the United States all of the east coast estuaries seem to have significant middle salinity regions.

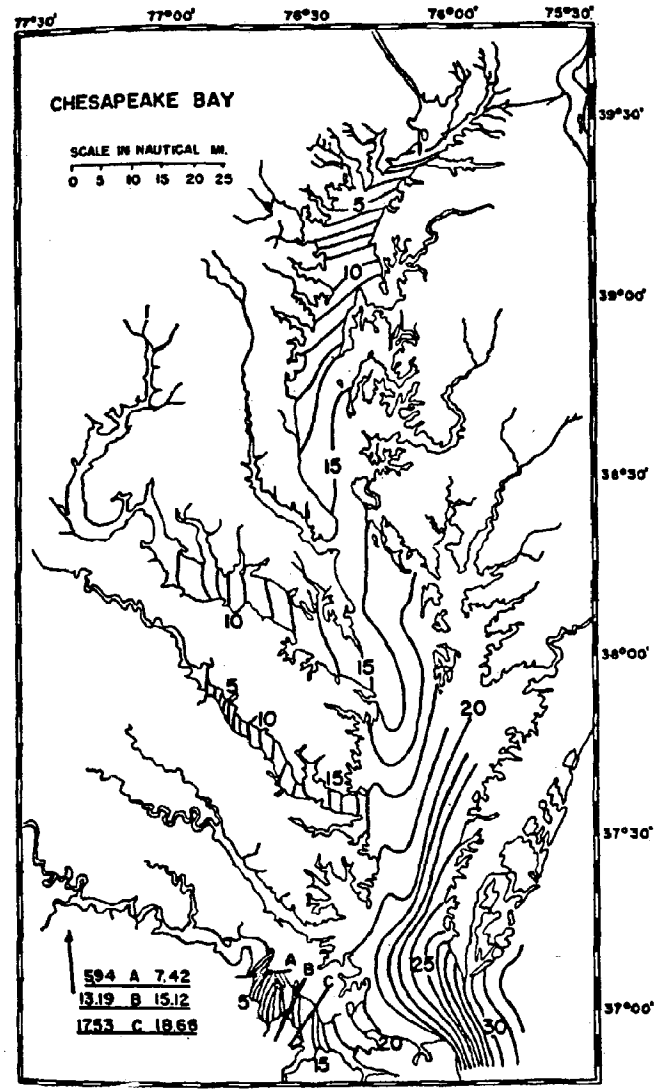
EXAMPLES

Chesapeake Bay

Chesapeake Bay is a coastal plain estuary and was formed by the drowning of former river valleys, either as a result of subsidence of the land or a rise in sea level. Pritchard (1952d) considered Chesapeake Bay to be an estuarine system composed of several estuaries of differing size and character but all draining into the lower Chesapeake Bay. The Chesapeake Estuarine System appears as an elongate indention of the Atlantic Coastline (Fig. 1). Tributary estuaries are formed by freshwater inflow from the Susquehanna, Potomac, James, Rappahannock, and York rivers. Tidal effects and brackish water intrusion penetrate sixty miles up the Potomac, nearly to Washington, D. C. (Fig. 2). If the upper limit of the estuarine system is taken as the mean limit of measurable salt water intrusion, then the area of the Chesapeake Bay System approaches 3,000 square miles (nautical). Surface salinity values at the



The Chesapeake Bay Estuarine System. Heavy line is 20-foot contour. Black areas represent depths greater than 60 feet.



Typical surface salinity pattern in Chesapeake Bay and tributary estuaries.

Fig. 1 and 2. Chesapeake Bay and salinities (Pritchard, 1952a).

same point in the James River were found to vary only about 4% between high and low tides. Most of Chesapeake Bay is shallow; 50% of the system is less that 20 feet deep. Shallow portions tend to be well mixed. Circulation in the James River was two layered. Net flow at depths greater than seven to eleven feet was generally upstream (Fig. 3).

Yaquina Estuary, Oregon

The plankton of the middle section of Yaquina Estuary in Oregon (Figs. 4-7) was compared with zones of similar salinity regime in New England by Frolander (1964) reporting Acartia copepod populations in both. The diurnal migration of plankton results in movements with the tide that tend to keep the population in the estuary (Fig. 4).

San Francisco Bay System

Intermediate zones of the Sacramento River estuary into San Francisco Bay are of middle salinity type (Fig. 7). Some representative data are given in Fig. 8 by Bain and McCarty (1965).

Galveston Bay

In the Gulf of Mexico, main parts of Galveston Bay are examples of the middle salinity plankton system (Fig. 9). Representative data are given in Figs. 10-13. Other estuarine systems which have been sufficiently studied to permit comparisons are Narragansett Bay, Long Island Sound, Delaware Bay, and the North Carolina Sounds. Although there are many differences among these systems, the middle salinity portion is, in many ways, similar in each. The Chesapeake Bay was selected for the main discussion.

DISCUSSION

Boundaries of the System

Precise delimitation of the geographical boundaries of the middle estuary is not possible because of the spatial and temporal variability exhibited by such components as characteristic biological associations and physico-chemical factors. Here the environment is a moving mass of water which may exist for a while as an independent, more or less homogeneous, patch or slug, while at another time, it may mix with other patches and form a larger homogeneous mass.

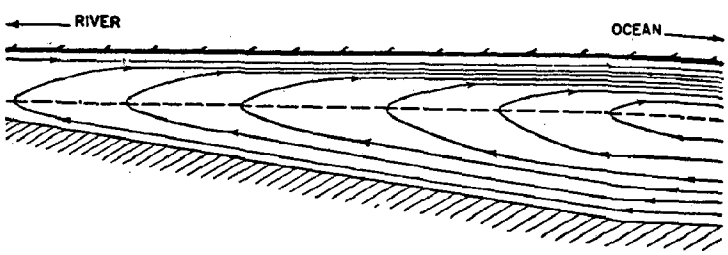
Wiebe and Holland (1968) used a computer model to study the accuracy and precision of net plankton samples. Application of the results of this work to thirteen actual field studies indicated that the 95% confidence limits usually exceed half or double the observed value regardless of the type of net, method of towing, or organisms used in the calculation. Advection, convection, and swimming movements of the organisms were suggested as energy

Table 1. Fish catch in Clear Lake, an arm of Galveston Bay, Texas (Chin and Inglis, 1960)

Golden croaker (*Micropogon undulatus*)	17,380
White shrimp (*Penaeus setiferus*)	13,840
Brown shrimp (*P. aztecus*)	7,123
Gulf menhaden (*Brevoortia patronus*)	2,846
Southern bay anchovy (*Anchoa mitchilli diaphana*)	2,726
Blue crab (*Callinectes sapidus*)	2,144
Spot croaker (*Leiostomus xanthurus*)	1,600

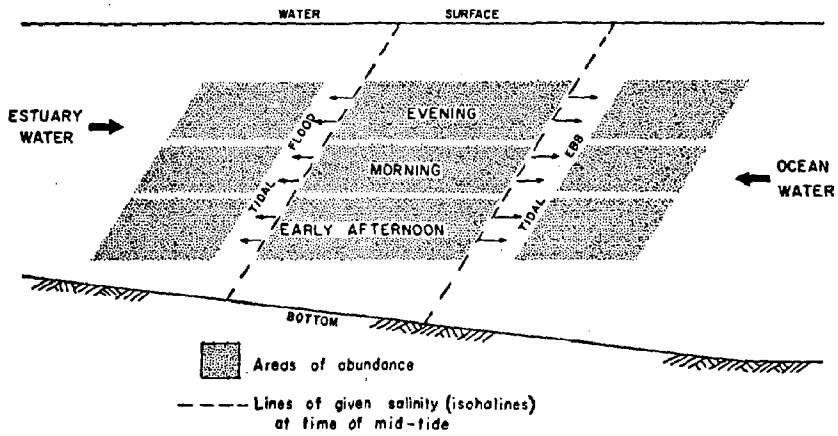
Six taken in lesser numbers were considered as minor species:

Sand squeteague (*Cynoscion arenarius*)	674
Hardhead catfish (*Galeichthys felis*)	321
Southern flounder (*Paralichthys lethostigma*)	272
Gafftopsail catfish (*Bagre marina*)	266
Hogchoaker (*Trinectes maculatus*)	224
Spotfin whiff (*Citharichthys spilopterus*)	150



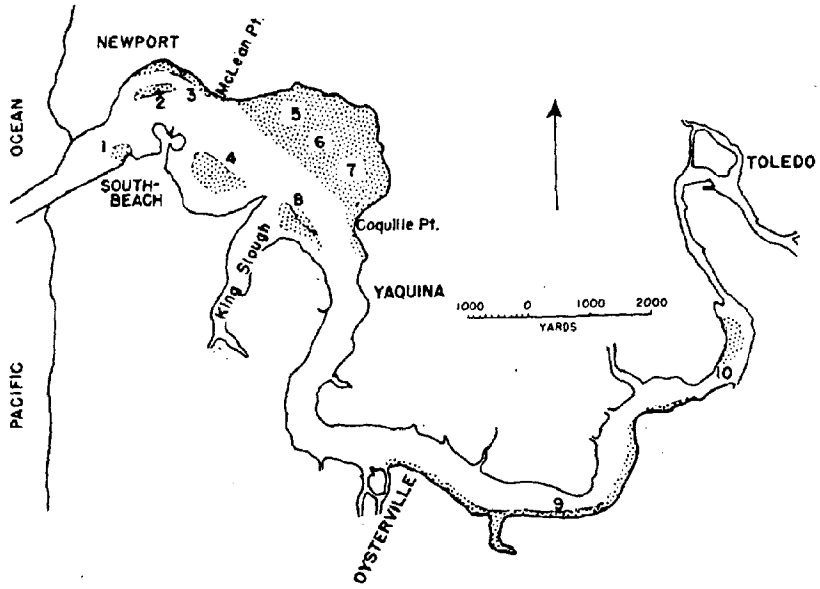
Schematic presentation of streamlines in a longitudinal section down central axis of the estuary.

Fig. 3. Circulation patterns from Pritchard (1952a).



Nine hypothetical positions that might be assumed by an estuarine zooplankton population influenced by tidal phase and time of day while remaining within a given salinity range.

Fig. 4. Copepod population positions in shifting tidal waters (Frolander, 1964).



Yaquina Bay

Fig. 5. Yaquina Estuary, Oregon. The middle salinity plankton system is the unshaded part of the lower estuary (Marriage, 1958).

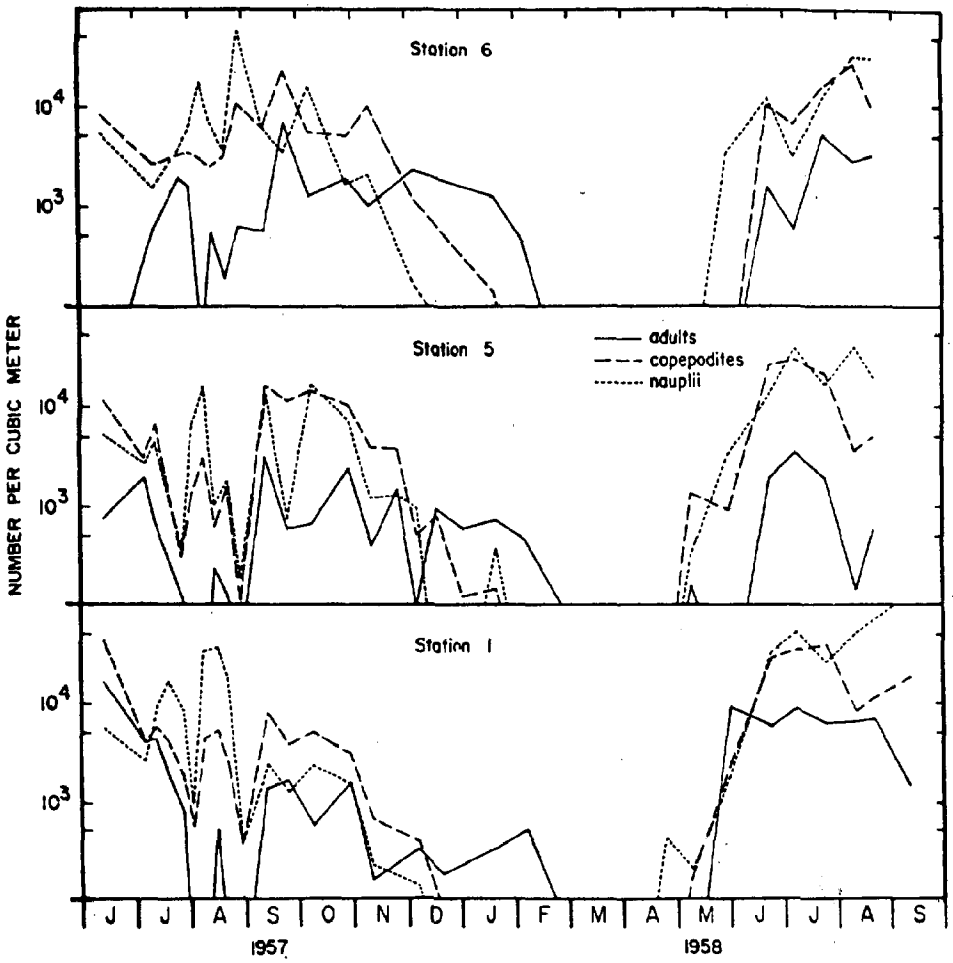


FIG. 4. Seasonal distribution of *A. tonsa* adults, immature copepodites, and nauplii at stations 1, 5, and 6 in Raritan Bay. 1957–58.

Fig. 6. Seasonal record of copepods of middle salinity system in Raritan Bay, New Jersey (Jeffries, 1962e).

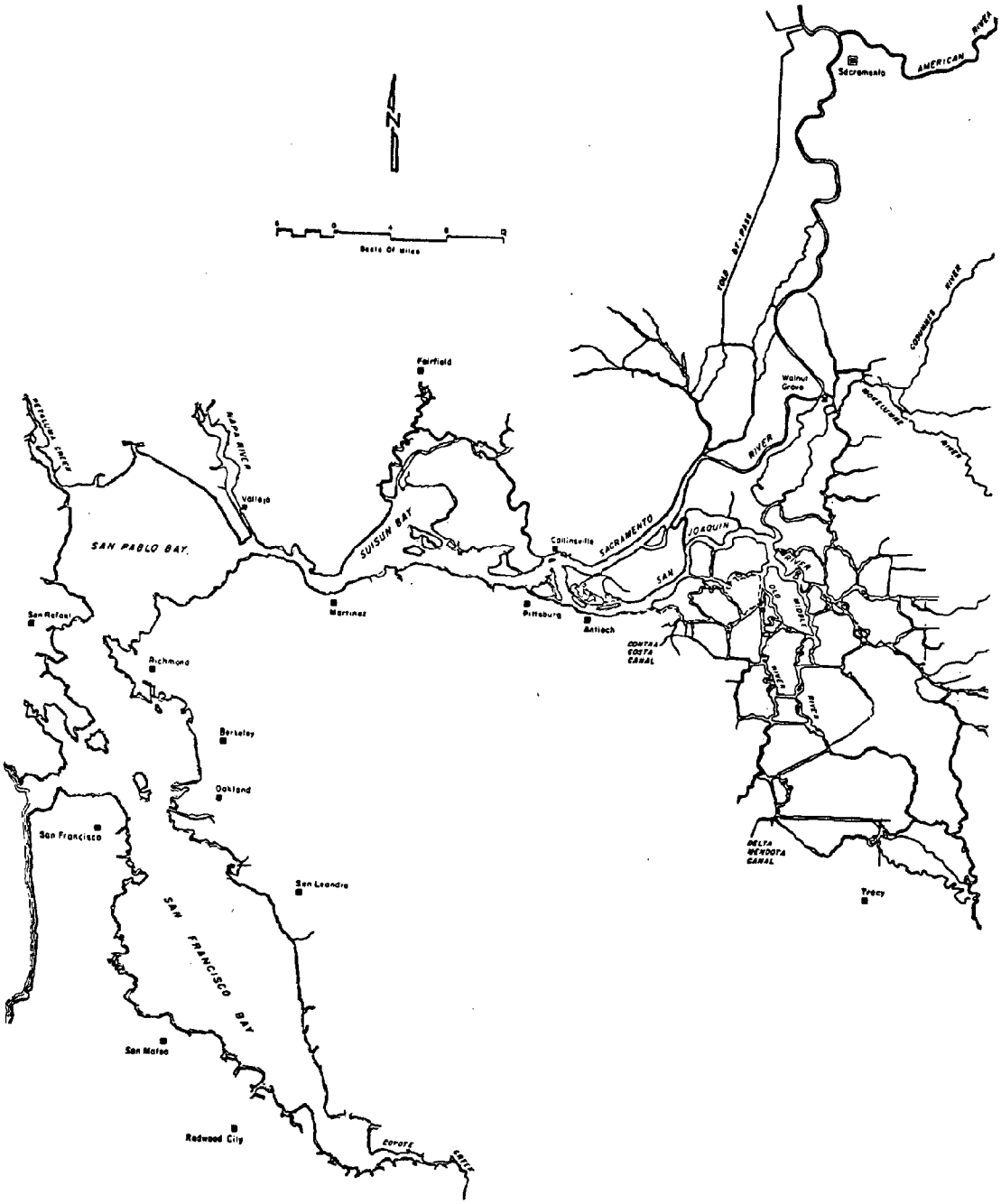


Fig. 7. Sacramento River - San Francisco Bay System (Orlob, Shubinski, and Feigner, 1967).

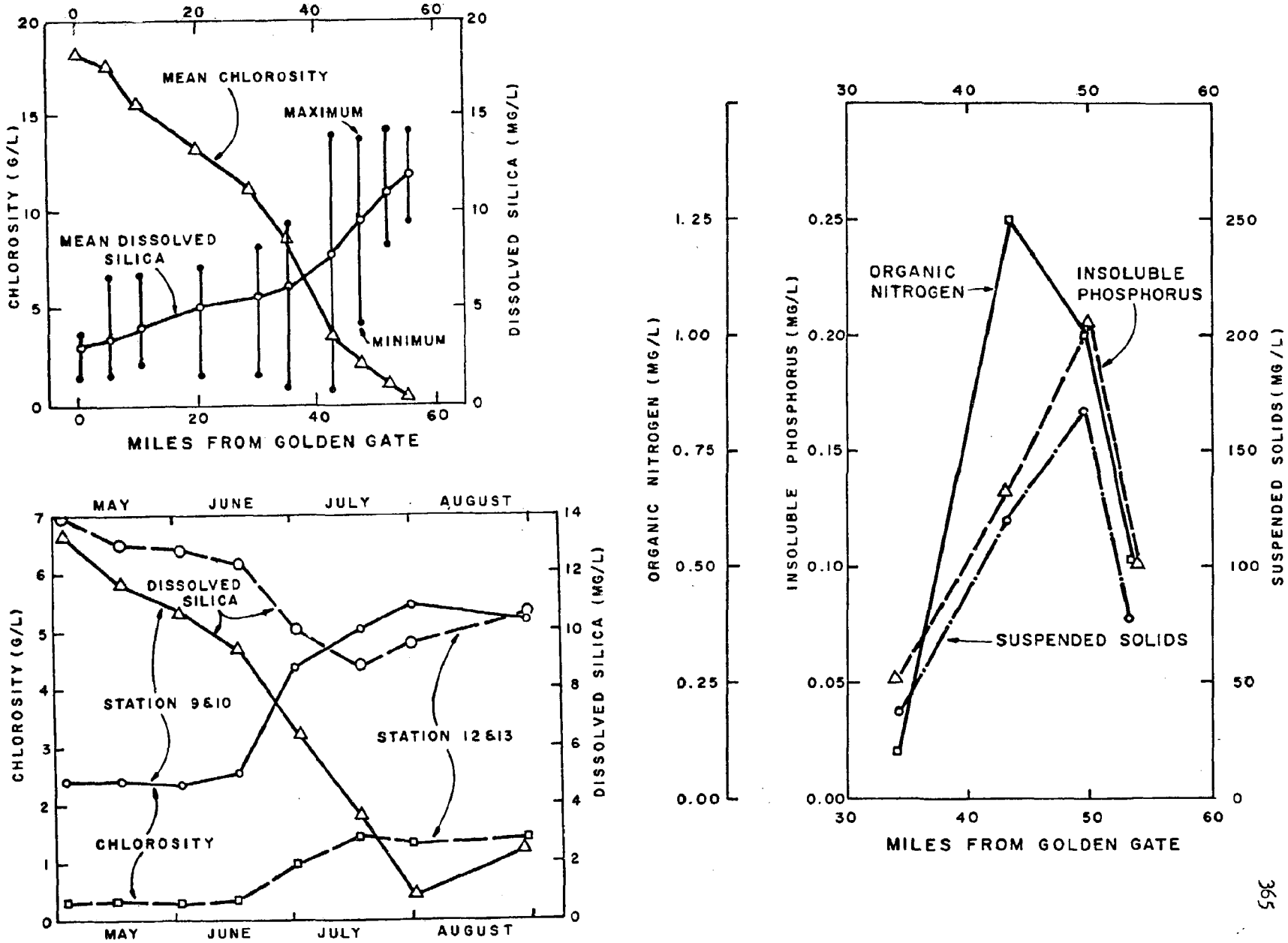


Fig. 8. Characteristics of the San Francisco Bay Estuary (Bain and McCarty, 1965). The middle salinity system is between 20 and 40 miles from the Golden Gate.

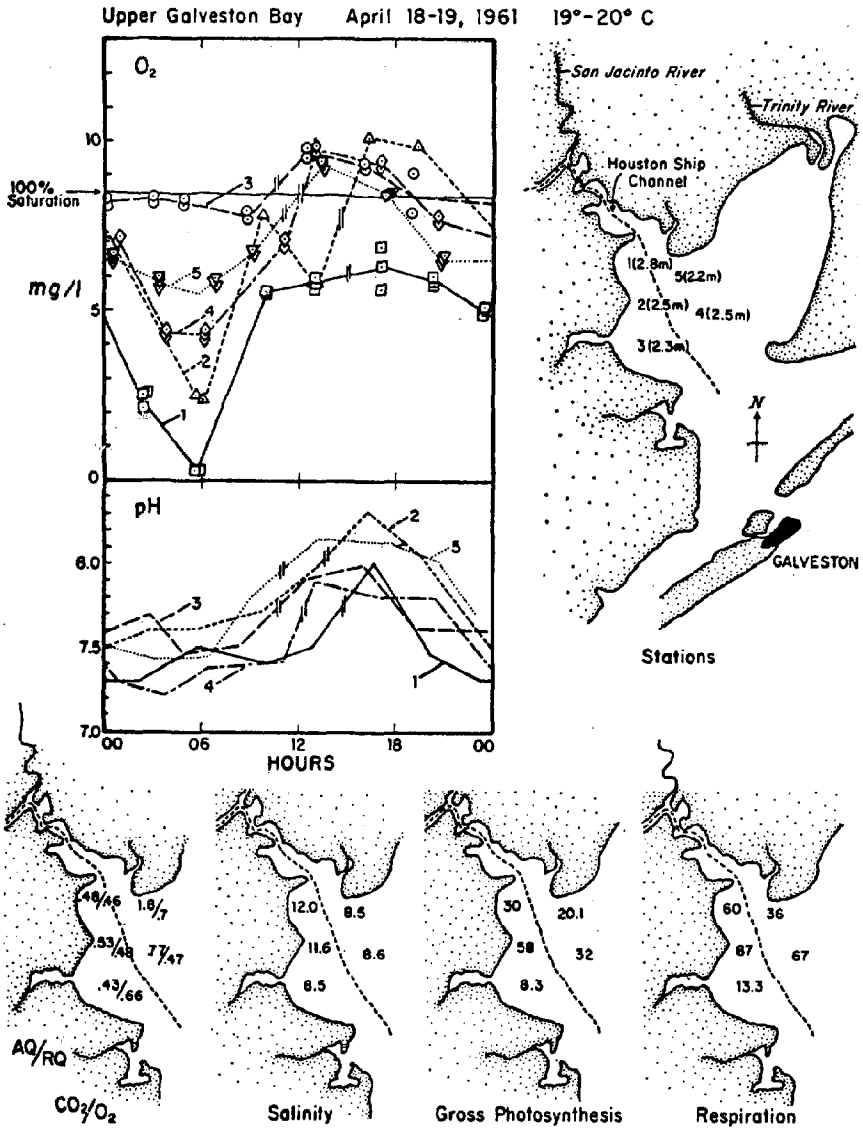
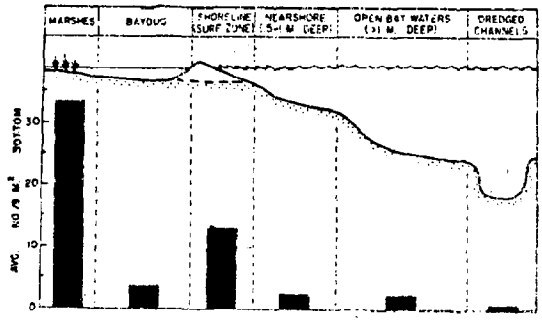


FIG. 5. Distribution of variables in Upper Galveston Bay, April 18–19, 1961 including diurnal record of oxygen, pH, and derived quantities.

Fig. 9. Productivity and respiration in g/m^2/day from diurnal records of oxygen and acidity (in Galveston Bay, Texas (Odum, Cuzon, Beyers, and Allbaugh, 1963).



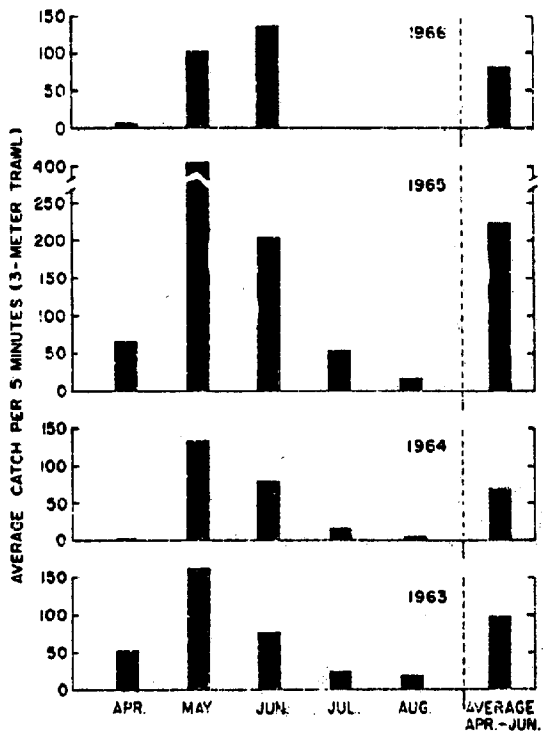
--Relative importance of different types of habitat in the Galveston estuary as nursery areas for juvenile brown shrimp, March-August 1965.

Fig. 10. Young shrimp in shallow nursery ground (Chapman, Trent, Mock, Pullen, Ringo in Lindner, 1967).

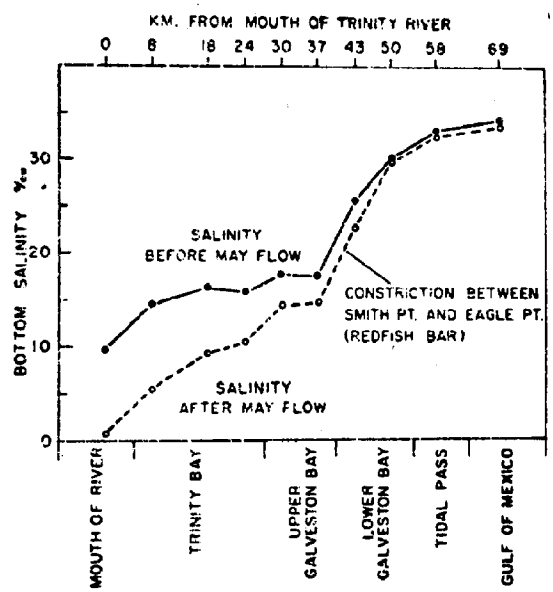
TABLE II

Comparison of the Most Abundant Species in the Total Catch by All Gear for 1954 and 1955. Figures represent per cent of total fish catch.

Species	1954	1955
Micropogon undulatus	42.2	8.3
Leiostomus xanthurus	20.2	5.8
Anchoa m. diaphana	15.9	67.1
Brevoortia patronus	7.1	8.8
Lagodon rhomboides	4.1	.5
Polydactylus octonemus	2.2	0.0
Cynoscion arenarius	1.9	1.7
Cyprinodon variegatus	1.1	.3
Mugil curema	.9	2.1
Sphoeroides nephelus	.9	.4
Galeichthys felis	.7	.8
Mugil cephalus	.5	.9
Bairdiella chrysura	0.0	.7
Total	97.7	97.4

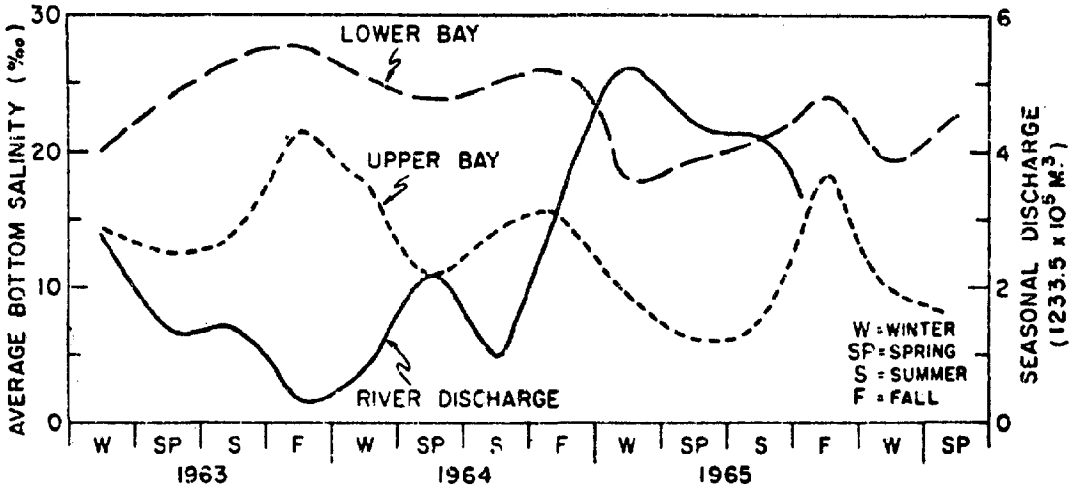


--Relative abundance of juvenile brown shrimp in the Galveston estuary.



--Effect of May 1963 Trinity River flow (5.8×10^6 m.^{3}) on salinity of Galveston estuary.

Fig. 11. Salinities, salinity changes during spring flood, and young brown shrimp during spring growth and emigration (Chapman, Trent, Mock, Pullen and Ringo in Lindner, 1967).



Influence of seasonal trends in Trinity River discharge on salinity in the upper (Trinity) and lower (lower Galveston) bays of the Galveston estuary.

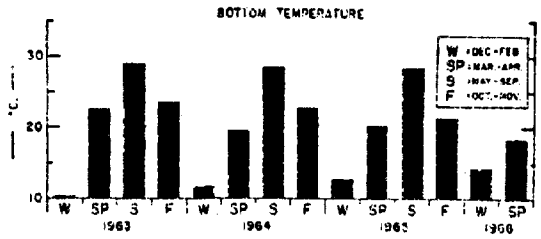
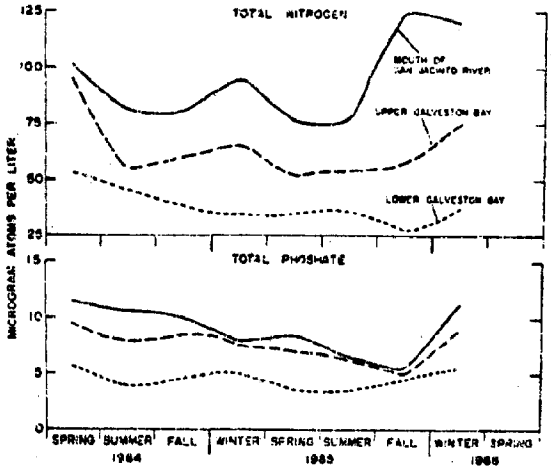
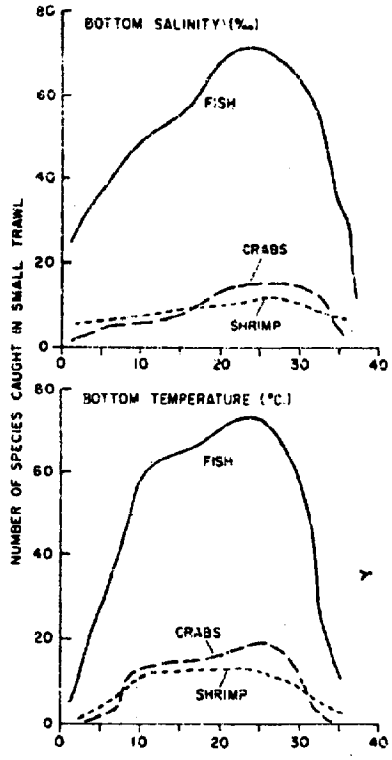


Figure 18.--Seasonal trends in water temperature in the Galveston estuary.

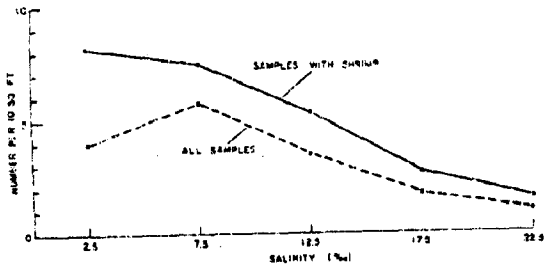


Influence of pollution from the upper Houston Ship Channel (mouth of San Jacinto River) on upper and lower Galveston Bays as indicated by seasonal trends in total nitrogen and total phosphate.

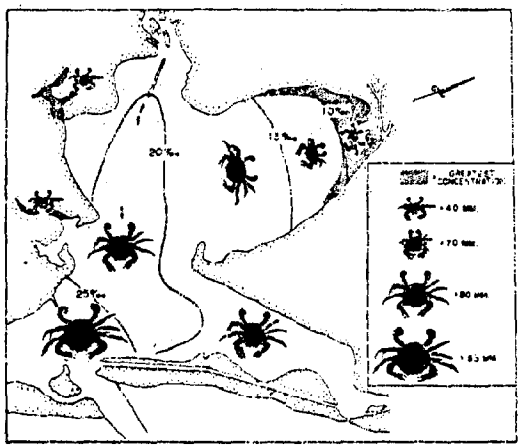


--Diversity of species of fish, crab, and shrimp in relation to temperature and salinity in the Galveston estuary.

Fig. 12. Salinities, nutrients, and some estimates of diversity in Galveston Bay, Texas (Chapman, Trent, Mock, Pullen and Ringo in Lindner, 1967).



Density of juvenile brown shrimp in Galveston Bay marshes in relation to salinity, 1965.



Average size (carapace width) of blue crabs in relation to salinity in the Galveston estuary.

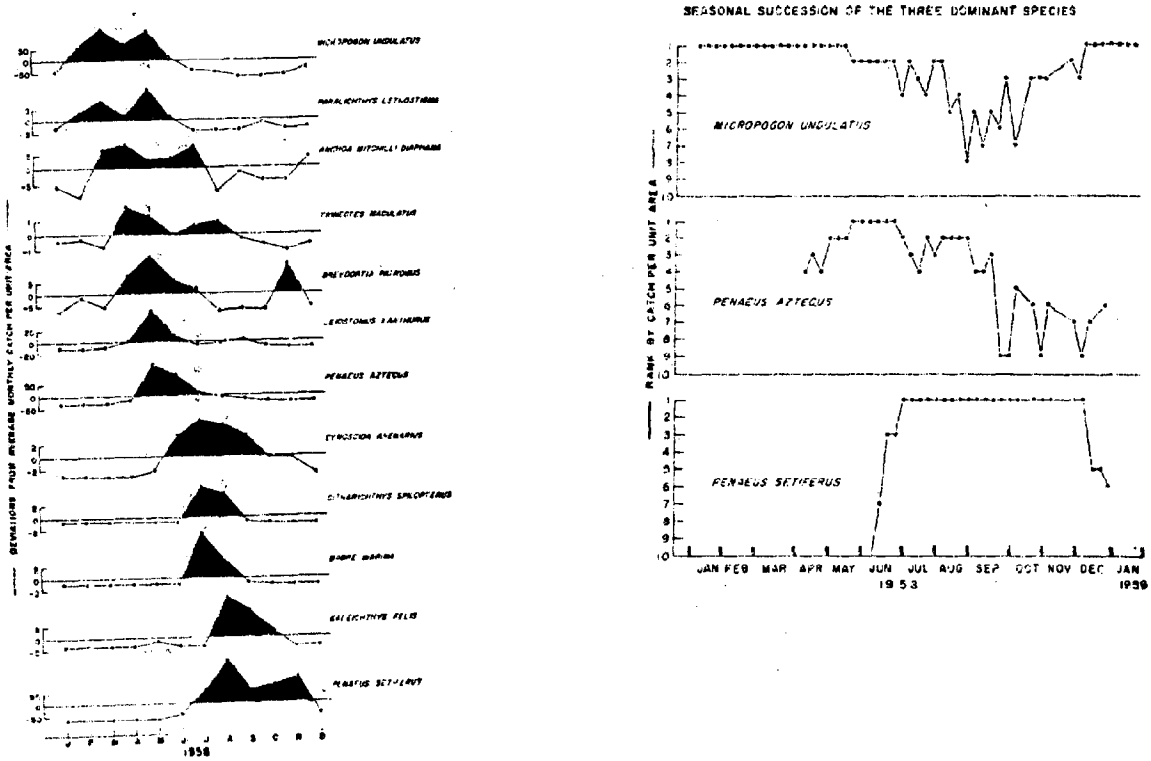


Fig. 13. Seasonal succession of fishes, crabs, and shrimp in Galveston Bay Texas (Chapman, Trent, Mock, Pullen, Ringo in Lindner, 1967).

changes tending to keep patches in a constant state of flux.

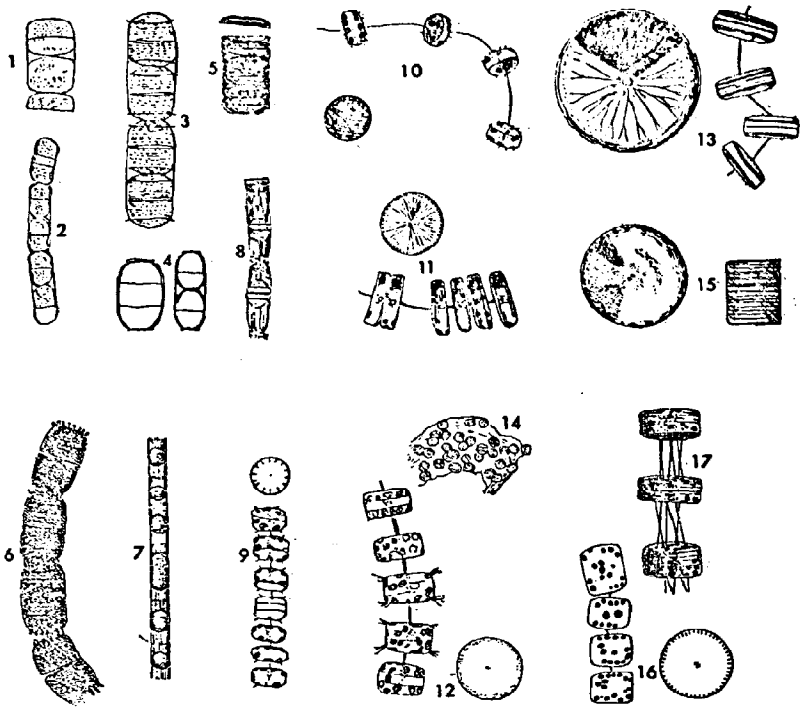
The middle estuary may vary from a state of great uniformity in chemical and biotic composition to a state in which highly distinctive patches form a mosaic of different sizedpieces variously having well-defined or ill-defined interfaces. Marked population variations between short time periods in the phytoplankton of Willoughby Bay and Hampton Roads, with the sudden appearance of another dominant form together with changing salinity values at various levels, was interpreted by Marshall (1967a) as results obtained from different water masses that possess different phytoplankton communities. The importance of wind in relation to salinity distribution, especially in shallow estuaries, has been noted by Barlow (1956). In Great Pond, variations in salinity distribution were closely related to day-to-day changes in wind force and direction. General seasonal change in salinity paralleled general changes in prevailing winds.

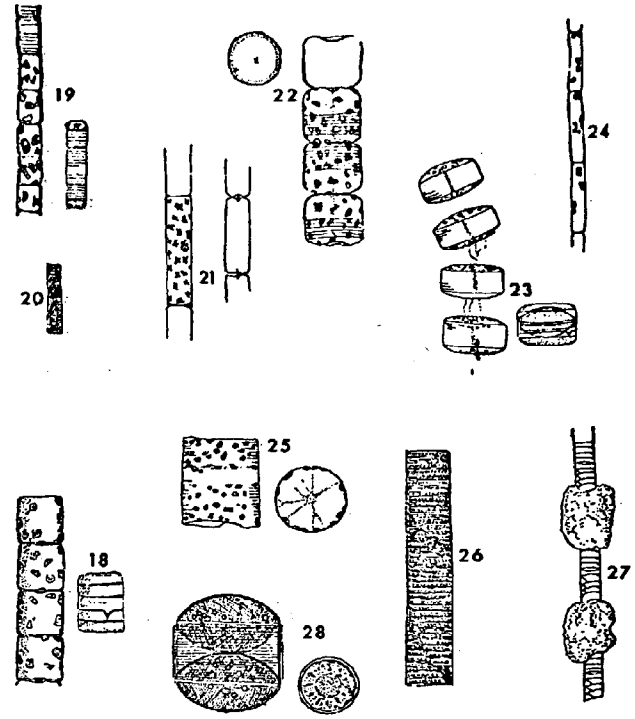
The biota of the middle estuary is generally comparable to that of other aquatic systems in that fish, invertebrates, and plankton are the dominant life forms. Whereas fish and most of the invertebrates can move across the interface between patches, the plankton organisms cannot. Distribution of the plankton might be expected to show generally greater variability within the system than that of non-plankton components. Phytoplankton are the primary producers within the system and certain plankton associations are its most constant biological feature.

Diatoms (Figs. 14, 15) and dinoflagellates (Fig. 16) are microscopic phytoplankton which are normally present in enormous numbers in estuarine waters. Both groups utilize light energy to reduce dissolved carbon dioxide to the form of oils or carbohydrates which are either stored as "food reserves" or incorporated as integral structural components of the cells which synthesized them. In either case the carbon fixed by these tiny plants can be ingested by barely visible invertebrate zooplankton such as calanoid copepods (Fig. 17). In this way inorganic carbon is converted to organic biomass and moved upward in increasingly larger accumulations as small animals are consumed by bigger ones. Intermediate consumers of the estuary include amphipods, arrow worms (Fig. 18), and fish larvae (Fig. 19).

The boundaries of the middle estuary must be considered in terms of characteristic plankton assemblages and the range in environmental conditions over which they thrive.

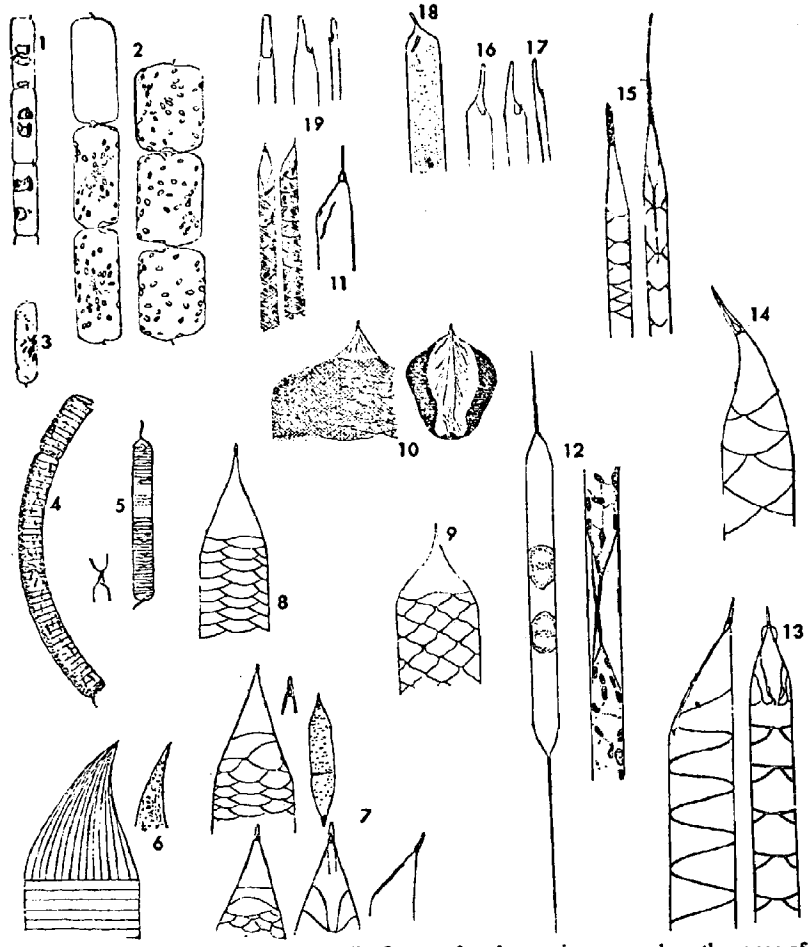
Barlow (1955b) described the essence of the interdependence between estuarine plankton and its environment when he stated that, "The maintainance of an endemic plankton population depends primarily on the dynamic balance between two processes: the translocation and dispersion of the population by water movements, and the reaction of the population to changes in environment caused by water movements."

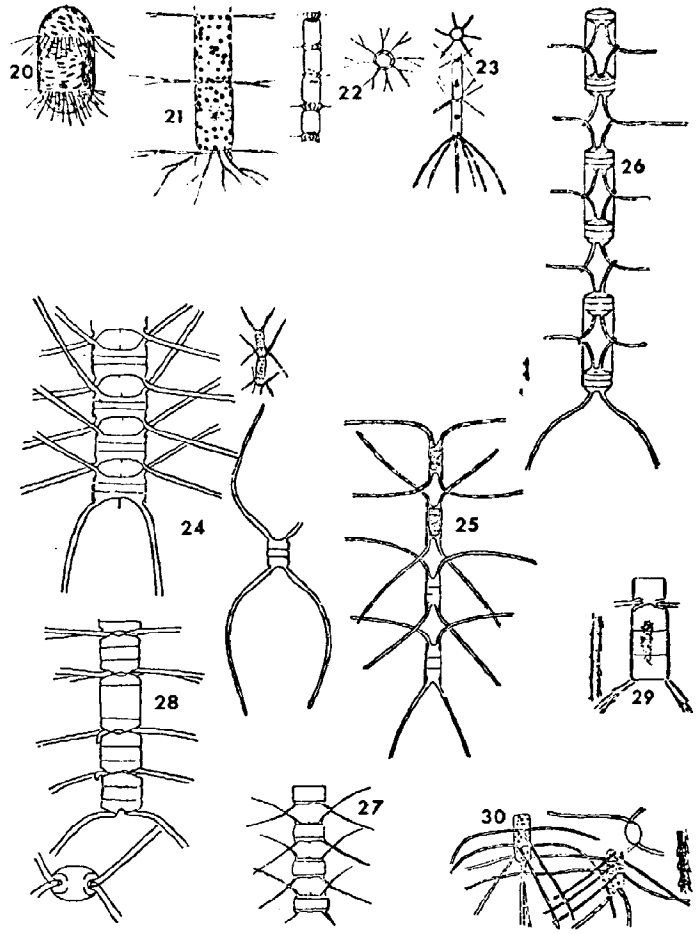




Marine diatoms. The figures after the species names show the range of cell-diameters in microns. (1) *Melosira borreri* Grev., 25–60. (2) *Melosira juergensis* Ag., 6–35. (3) *Melosira nummuloides* (Dillw.) 12–33. (4) *Melosira hyperborea* (Grun.), 14–30. (5) *Paralia sulcata* (Ehbg.), 16–45. (6) *Stephanopyxis turris* (Grev.), 35–65. (7) *Skeletonema costatum* (Grev.), 7–16. (8) *Skeletonema mirabile* Grun., 15. (9) *Thalassiosira nordenskjoldii* Cleve, 12–43. (10) *Thalassiosira decipiens* (Grun.), 12–40. (11) *Thalassiosira hyalina* (Grun.), 16–42. (12) *Thalassiosira gravida* Cleve, 17–62. (13) *Thalassiosira baltica* (Grun.), 60–120. (14) *Thalassiosira subtilis* (Ostenf.), 16–32. (15) *Thalassiosira bioculata* (Grun.), 60–30. (16) *Thalassiosira condensata* (Cleve), 25–30. (17) *Coscinosira polychorda* (Gran), 24–76. (18) *Bacteriosira fragilis* (Gran), 18–20. (19) *Detonula cystifera* (Gran), 6·5–15. (20) *Detonula confervacea* (Cleve), 10. (21) *Detonula schroderi* (P. Bergon), 22–28. (22) *Lauderia borealis* Gran, 34–47. (23) *Lauderia glacialis* (Grun.), 36–64. (24) *Leptocylindrus danicus* Cleve, 6–11. (25) *Guinardia flaccida* (Castr.), 42–90. (26) *Dactyliosolen antarcticus* Castr., 38–60. (27) *Dactyliosolen tenuis* Cleve, 10–25. (28) *Hyalodiscus stelliger* Bail., 35–85.

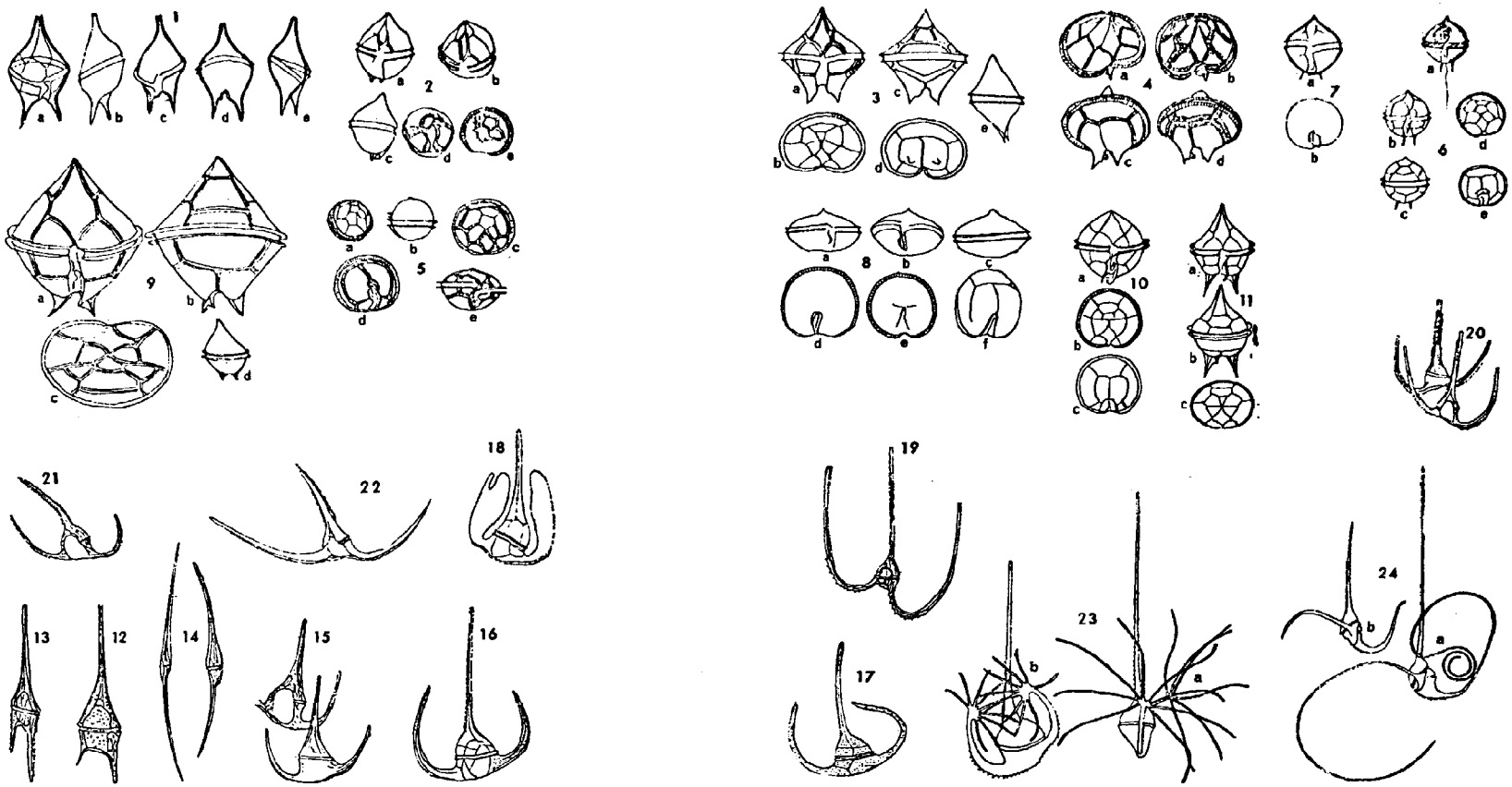
Fig. 14 Marine phytoplankton (Wimpenny, 1966)





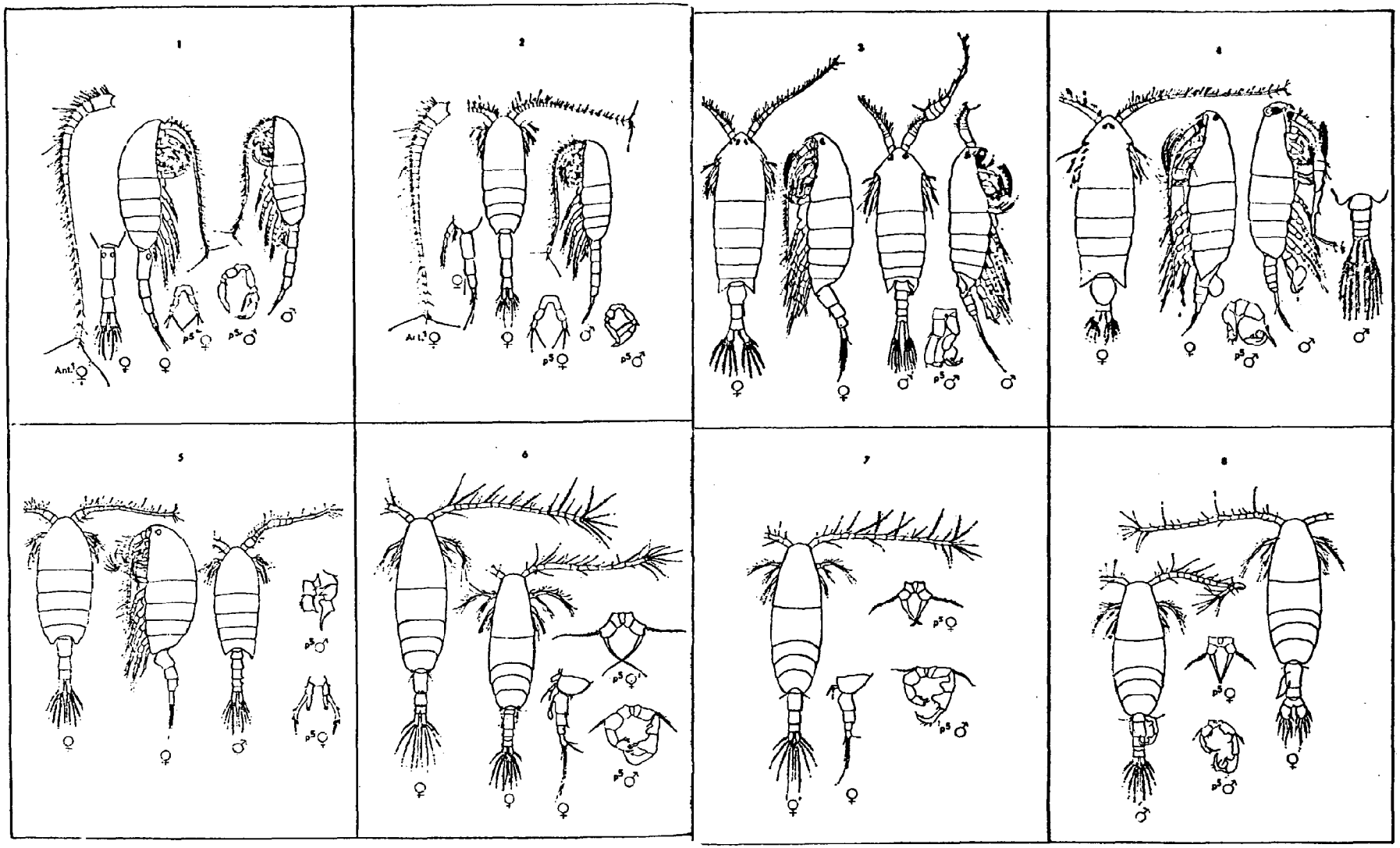
Marine diatoms. The figures after the species names show the range of the cell-diameters in microns. (1) *Rhizosolenia delicatula* Cleve, 14–20. (2) *Rhizosolenia faroensis* Ostenf., 40–70. (3) *Rhizosolenia fragillima* Bergon, 20. (4) *Rhizosolenia stolterfothi* H. Perag., 15–40. (5) *Rhizosolenia cylindrus* Cleve, 26. (6) *Rhizosolenia robusta* Norman, 160–170. (7) *Rhizosolenia acuminata* (Perag.), 35–50. (8) *Rhizosolenia bergonii* H. Perag., 100. (9) *Rhizosolenia castracanii* H. Perag., 150. (10) *Rhizosolenia arafurensis* Castr., 120. (11) *Rhizosolenia shrubsolii* Cleve, 12–32. (12) *Rhizosolenia setigera* Brightw., 10–25. (13) *Rhizosolenia styliformis* Brightw., 22–102. (14) *Rhizosolenia calcar-avis* Schultze, 30–60. (15) *Rhizosolenia hebetata* Bail., 4·5–12·5. (16) *Rhizosolenia alata* Brightw., 7–15. (17) *Rhizosolenia alata* f. *gracillima* (Cleve) Grunow, 5–7. (18) *Rhizosolenia alata* f. *indica* (Perag.) Ostenf., 48. (19) *Rhizosolenia obtusa* Hensen, 5–13. (20) *Corethron criophilum* Castr., 20–30. (21) *Bacteriastrum varians* Lauder, 20–40. (22) *Bacteriastrum delicatulum* Cleve, 12. (23) *Bacteriastrum elongatum* Cleve, 7–10. (24) *Chaetoceros atlanticum* Cleve, 15–20. (25) *Chaetoceros neapolitanum* Schroder, 13. (26) *Chaetoceros dichaeta* Ehr., 20–45. (27) *Chaetoceros polygonum* Schutt, 12–15. (28) *Chaetoceros densum* Cleve, 10. (29) *Chaetoceros coarctatum* Lauder, 20–40. (30) *Chaetoceros tetrastichon* Cleve, 10.

Fig. 15. Marine Phytoplankton (Wimpenny, 1966)



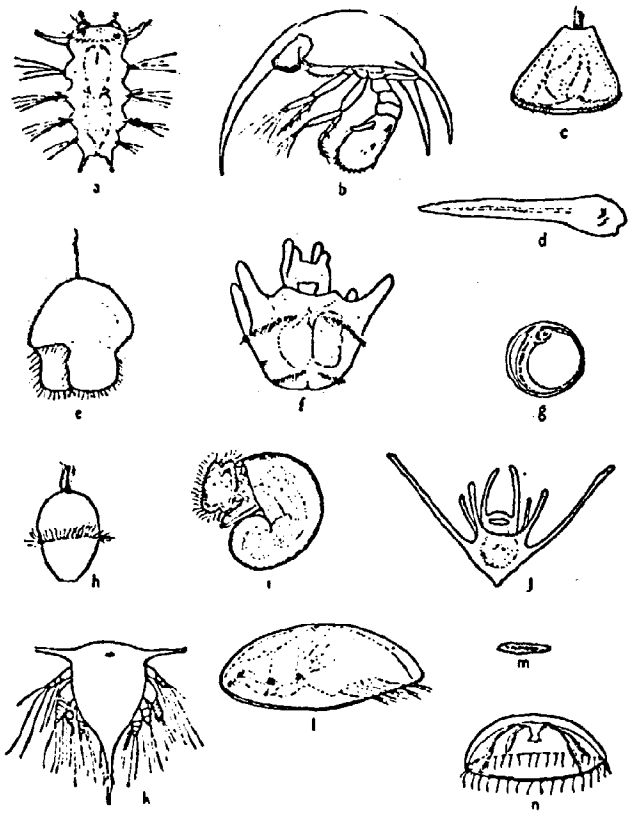
Peridinians. The figures after the species names show the apical to antapical lengths in microns except where otherwise stated. (1) *Peridinium oblongum* (Aurivillius), 110–117. (a) Ventral. (b) Right side. (c) Ventral. (d) Dorsal. (e) Right side. (2) *Peridinium piriforme* Paulsen, 42–70. (a) Ventral. (b) Ventro-apical. (c) Right side. (d) Apical. (e) Antapical. (3) *Peridinium divergens* Ehbg., 80–84. (a) Ventral. (b) Apical. (c) Dorsal. (d) Antapical. (e) Right side. (4) *Peridinium curtipes* Jorgensen, 80–90. (a and b) Apical. (c and d) Dorsal-antapical. (5) *Peridinium globulus* Stein, 50–78. (a and c) Apical. (b) Side. (d) Antapical. (e) Ventral. (6) *Peridinium cerasus* Paulsen, 30–40 (width). (a) Alive. (b) Ventral. (c) Dorsal. (d) Apical. (e) Antapical. (7) *Peridinium roseum* Paulsen, 50–58 (without spines). (a) Ventral. (b) Antapical. (8) *Peridinium decipiens* Jorgensen, 44–56. (a and b) Ventral. (c) Dorsal. (d and f) Antapical. (e) Apical. (9) *Peridinium pallidum* Ostenfeld, 70–96. (a) Ventral. (b) Dorsal. (c) Apical. (d) Side. (10) *Peridinium curvipes* Ostenfeld, 48–52. (a) Ventral. (b) Apical. (c) Antapical. (11) *Peridinium diabolus* Cleve, 50–70. (a) Ventral. (b) Dorsal. (c) Apical. (12) *Ceratium furca* (Ehbg.), 30–50 (width). (13) *Ceratium lineatum* (Ehbg.), 25–47 (width). (14) *Ceratium fusus* (Ehbg.), 15–30 (width). (15) *Ceratium tripos* (O.F.M.) Nitzsch var. *atlantica* f. *neglecta* Ostenfeld, 73–95 (width). (16) *Ceratium bucephalum* (Cleve), 54–64 (width). (17) *Ceratium bucephalum* (Cleve) var. *heterokamptum* (Jorg.), 176. (18) *Ceratium platycorne* Daday, 48–64 (width). (19) *Ceratium macroceros* (Ehbg.), 45–57 (width). (20) *Ceratium horridum* Gran, 42–57 (width). (21) *Ceratium longipes* (Bail.) Gran, 51–57 (width). (22) *Ceratium arcticum* (Ehbg.) Cleve, 48–60 (width). (23) *Ceratium palmatum* Schroder [*Ceratium ranipes* Cleve], (a) Indian Ocean type, 452. (b) Atlantic Ocean type, 330. (24) *Ceratium reticulatum* (Pouchet) Cleve f. *spiralis* Kofoid, [*Ceratium hexacanthum* Gourret f. *spiralis* Kofoid], (a) Indian Ocean type, 900. (b) Atlantic Ocean type, 400.

Fig. 16. Marine Phytoplankton dinoflagellates (Wimpenny, 1966).



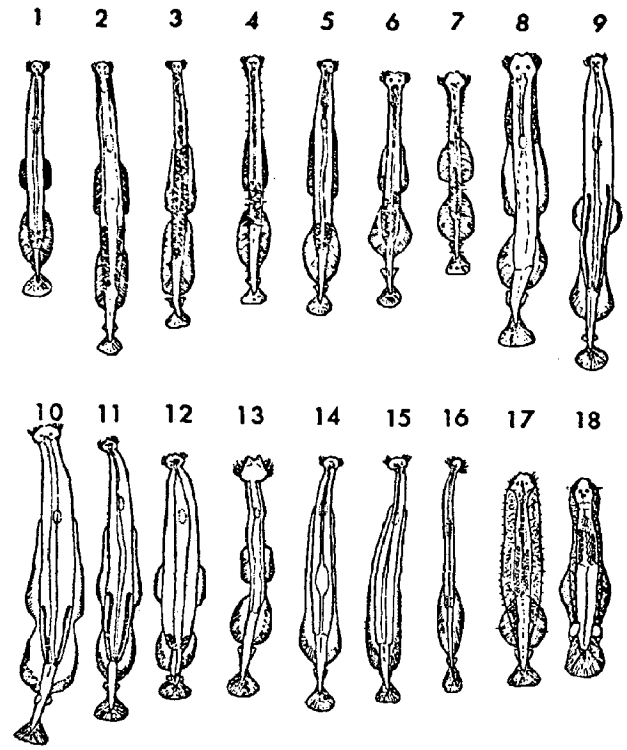
Calanoid copepods. The figures after the species name represent the animals' lengths in millimetres. (1) *Metridia longa* (Lubbock), ♀, 4·3, ♂, 3·7. (2) *Metridia lucens* Boeck, ♀, 2·5, ♂, 2·3. (3) *Anomalocera patersoni* Templeton, ♀, 3·2, ♂, 3·0. (4) *Labidocera wollastoni* Lubbock, ♀, 2·4, ♂, 2·2 (5) *Parapontella brevicornis* (Lubbock), ♀, 1·55, ♂, 1·35. (6) *Acartia longiremis* (Lilljeborg), ♀, 1·25, ♂, 1·05. (7) *Acartia clausi* Giesbrecht, ♀, 1·15, ♂, 1·0. (8) *Acartia discaudata* Giesbrecht, ♀, 1·2, ♂, 1·1.

Fig. 17. Marine Zooplankton Copepods (Wimpenny, 1966).



Characteristic larvae of the meroplankton: (*a*) chaetate larva of the annelid *Platynereis agassizi*, (*b*) zoea of sand crab, *Emerita analoga;* (*c*) cyphonautes larva of bryozoa; (*d*) tadpole larva of sessile tunicate; (*e*) pilidium larva of nemertean worm; (*f*) advanced pluteus larva of sea urchin; (*g*) fish egg with embryo; (*h*) trochophore larva of scaleworm; (*i*) veliger larva of snail; (*j*) pluteus larva of brittle star; (*k*) nauplius larva of barnacle; (*l*) cypris larva of barnacle; (*m*) planula larva of coelenterate; (*n*) medusa of hydroid.

(Sverdrup, Johnson, and Fleming, 1942)



Arrow worms (*Chaetognatha*). The figure behind each species name is the usual maximum length in millimetres. (1) *Sagitta setosa* J. Müller, 20. (2) *Sagitta elegans* Verrill, 25. (3) *Sagitta serratodentata* Krohn, 17. (4) *Sagitta bipunctata* Quoy and Gaimard, 19. (5) *Sagitta friderici* R.-Z., 15. (6) *Sagitta decipiens* Fowler, 20. (7) *Sagitta hispida* Conant, 15. (8) *Sagitta zetesios* Fowler, 40. (9) *Sagitta hexaptera* d'Orbigny, 60. (10) *Sagitta maxima* (Conant), 90. (11) *Sagitta lyra* Krohn, 38. (12) *Sagitta enflata* Grassi, 30. (13) *Sagitta macrocephala* Fowler, 21. (14) *Eukrohnia hamata* (Möbius), 45. (15) *Eukrohnia fowleri* R.-Z., 40. (16) *Krohnitta subtilis* (Grassi), 16. (17) *Pterosagitta draco* (Krohn) 10. (18) *Spadella cephaloptera* (Busch), 4. Winged snails (*Pteropoda*). The figure behind the species name is the maximum dimension in millimetres for the entire animal. (19) *Limacina* (*Spiratella*) *helicina* (Phipps), 8. (20) *Limacina*

(Wimpenny, 1966)

Fig. 18. Zooplankton including larvae on the left and arrowworms on the right.

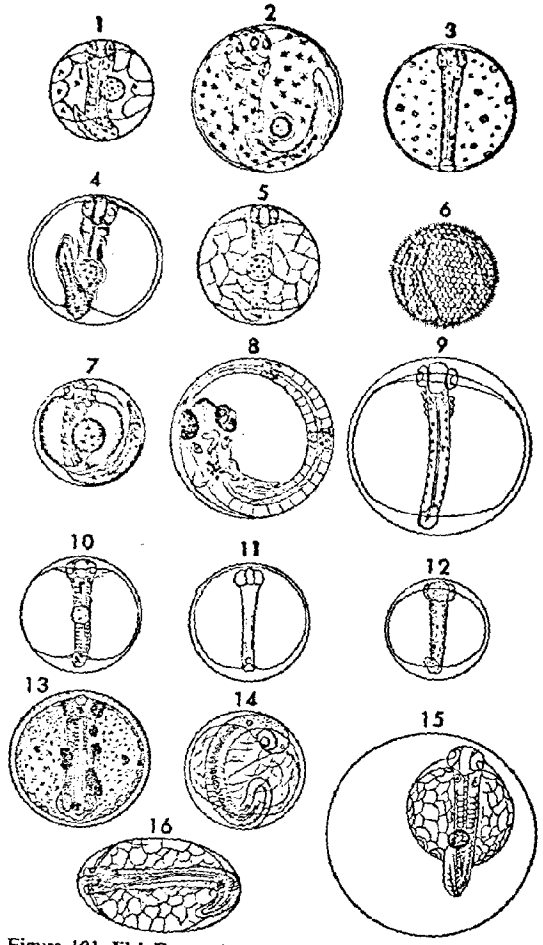


Figure 101. Fish Eggs. The figure after the Latin name is the diameter in millimetres. (1) Red mullet—*Mullus surmuletus* L., 0·87. (2) Grey gurnard—*Trigla gurnardus* L., 1·25. (3) Weaver—*Trachinus vipera* Cuv., 1·10. (4) Mackerel—*Scomber scombrus* L., 1·18. (5) Horse mackerel—*Caranx trachurus* L., 0·94. (6) Dragonet—*Callionymus lyra* L., 0·9. (7) Grey mullet—*Liza ramada* Risso, 1·0. (8) Cod—*Gadus morrhua* L., 1·35. (9) Haddock—*Gadus aeglefinus* L., 1·51. (10) Turbot—*Rhombus maximus* L., 1·10. (11) Plaice—*Pleuronectes platessa* L., about 2. (12) Dab—*Pleuronectes limanda* L., 0·85. (13) Sole—*Solea vulgaris* Quensel, 1·38. (14) Sprat—*Clupea sprattus* L., 1·006. (15) Pilchard—*Clupea pilchardus* Walb., 1·72. (16) Anchovy—*Engraulis encrasicolus* L., 1·37.

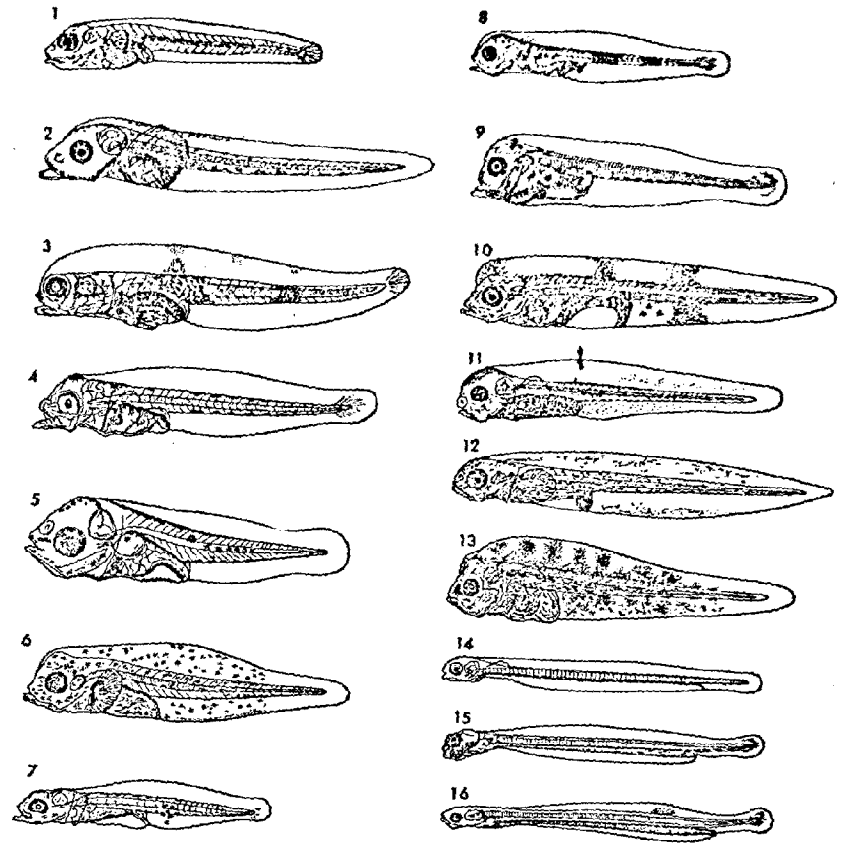


Figure 102. Fish Larvae. The figure after the Latin name is the length in millimetres. (1) Red mullet—*Mullus surmuletus* L., 4·5. (2) Grey gurnard—*Trigla gurnardus* L., 4·7. Six days old. (3) Weaver—*Trachinus vipera* Cuv., 3·5. (4) Mackerel—*Scomber scombrus* L., 4·5. About nine days old. (5) Horse mackerel—*Caranx trachurus* L., 4·7. Dragonet—*Callionymus lyra* L., 2·3. (7) Grey mullet—*Mugil* sp., 2·3. (8) Cod—*Gadus morrhua* L., 8. (9) Haddock—*Gadus aeglefinus* L., about 8. Eleven days old. (10) Turbot—*Rhombus maximus* L., 4·8. (11) Plaice—*Pleuronectes platessa* L., 7·5. (12) Dab—*Pleuronectes limanda* L., 4·3. Ten days old. (13) Sole—*Solea vulgaris* Quensel, 4·24. Eight days old. (14) Sprat—*Clupea sprattus* L., 4·7. Seven days old. (15) Pilchard—*Clupea pilchardus* Walb., 5·5. Nine days old. (16) Herring—*Clupea harengus* L., 10·5.

Fig. 19. Fish eggs and larvae (European forms from Wimpenny, 1966). Larvae of estuarine species in U.S. estuaries are similar.

System Components

In terms of actual numbers, as well as number of species, the great majority of estuarine plankton organisms belong to just four major groups. Calanoid copepods are the largest in size and adults may be just visible without magnification. Photosynthetic dinoflagellates and elongate diatoms are next in order of size and usually require magnification to be seen. Various algae, frequently flagellates, comprise the smallest members of the plankton. These nanoplankton are often missed by net sampling procedures although, in many situations, they form a very significant fraction of the photosynthetic biomass.

One general characteristic of plankton organisms of the middle estuary is that, while they may be volumetrically abundant, they tend to be limited with respect to species variety (Riley 1967a).

Hulburt (1963) defined dominance in terms of an index consisting of the combined concentration of the two most abundant species in a phytoplankton sample divided by the concentration of all species counted. Application of this index to estuarine areas in Long Island Sound gave average percentage dominance values of 81 to 95. In general, the greatest dominance was directly related to greater population density. Apparently higher nutrient levels in estuaries leads to enhanced growth of a few, or a single, especially well adapted forms which become dominant and thereby reduce diversity. Extremely shallow water may lead to even greater reduction in species diversity through settling of larger species.

Zooplankton. The calanoid copepod Acartia tonsa appears to be the most persistent and abundant zooplankter in the Chesapeake Bay. Heinle (1966) observed this copepod throughout the year in the Patuxent River estuary. Densities up to 10^5 cells m^3 were recorded during the warmer months at which time A. tonsa accounted for more than half of the crustacean zooplankton. Summer production was estimated to average about 1.7 lb/acre-day with growth from egg to egg taking 7, 9, and 13 days, respectively at 25.5, 22.4, and 15.5° C. At least half of the phytoplankton production was consumed by A. tonsa during the summer months. Both vertical and horizontal distribution were described as "patchy." Acartia tonsa is of comparable numerical importance in the Delaware River estuary (Cronin et. al. 1962), Biscayne Bay (Woodmansee 1958), Texas Gulf Coast (Brever 1957), Long Island Sound (Conover 1956) and the Cape Cod area (Deevey 1948 and Barlow 1955). During winter, in estuaries north of Cape Hatteras, Acartia clausi tends to replace Acartia tonsa (Riley 1967a). Martin (1968) has reported niche substitution of A. clausi for A. tonsa during winter and spring in Narrangansett Bay. In St. Andrew Bay on the Gulf Coast of Florida copepods made up 59% of the total number and 55.8% of the total zooplankton biomass (Hopkins 1966). In St. Andrew Bay copepod maxima occurred during the warmer months and zooplankton dominance was shared nearly equally between A. tonsa, which comprised 20% of the total (dry weight) zooplankton standing crop, and another calanoid copepod, Paracalanus, which amounted to 16% of the total catch. Acartia tonsa occurs from the Gulf of St. Lawrence to the Gulf of Mexico (Riley 1967a) and is perhaps the most characteristic biotic component of the middle estuary plankton.

Other important zooplankters associated with Acartia dominance are variable. Cronin et. al, (1962) reported that in Delaware Bay Eurytemora hirundoides, E. affinis, Pseudodiaptomus coronatus, and Neomysis americana, together with Acartia tonsa were resident species which made the estuarine zooplankton in the mesohaline region distinctly different from the ocean or the river. Oithona spp. were among the more important zooplankton in St. Andrew Bay (Hopkins 1966) or were among the principal grazers in Narragansett Bay (Martin 1965) in portions of these estuaries dominated by Acartia.

Phytoplankton. Diatoms and dinoflagellates are of comparable size and are usually collected and studied together. Essentially, these organisms constitute the "net phytoplankton." Riley (1967a) reported a total phytoplankton flora of 150 species for Long Island Sound. Weighting for consistency and relative dominance, he suggested that perhaps thirteen species could be considered "native" to the estuary. Of these thirteen species, nine were diatoms and four were dinoflagellates. Phytoplankton community structure is similar to that of the zooplankton in that a single species, the diatom Skeletonema costatum, is characteristically dominant. Concentrations of this diatom reaching 35 x 10^6 cells per liter were observed by Conover (1967) in Long Island Sound. The fact that the percentage composition of S. costatum is similar in several estuaries [Narragansett Bay, 81.2%, Smayda (1957), and 80.0%, Ferrara (1953); Block Island Sound, 83.5%, Riley (1952); and James River, 83% Marshall (1967a)] suggests that a "characteristic" estuarine phytoplankton structure is a real entity.

Diatoms. A variety of diatoms have been reported as associate species in situations where S. costatum is dominant. Important diatom associates in the Chesapeake Bay include species of Asterionella, Nitzschia, Rhizosolenia, Bacteriastrum (Patten et. al. 1963). Representatives of these genera, not necessarily the same species, are S. costatum associates in the James River (Marshall 1967a) and the York River (Fournier 1966). Hopkins (1966) reported species of Chaetoceros and Rhizosolenia as the dominants in St. Andrew Bay, but noted that these were "high salinity" species associated with the Gulf of Mexico. Skeletonema costatum was the dominant "intermediate salinity" species, 8.7% of the total diatom volume, while a species of Cyclotella was subdominant, 6.6% of the total diatom volume. Species of Coscinodiscus and Thalassionema were also considered by Hopkins to be characteristic of intermediate salinity portions of St. Andrew Bay. Asterionella japonica and Rhizosolenia fragilissima were diatoms of greatest secondary importance, 2.5 and 3.1 percent of the total, respectively, after Skeletonema costatum (81.2% of the total) in Narragansett Bay (Smayda 1957).

The diatom flora of the middle estuary is diverse and varies seasonally as well as geographically. Even so, Skeletonema costatum is frequently overwhelmingly dominant and important associate species, while variable, represent relatively few genera. Many estuarine diatoms may be strays which

achieve success only on rare occasions. By considering only species that were well enough suited to the environment to be significant in normal patterns of seasonal periodicity, Riley (1967a) reduced the important diatoms of Long Island Sound to six genera including nine species: Skeletonema costatum, Thalassionema nitzschioides, Paralia (Melosira) sulcata, Schroderella delicatula, Thalassiosira decipiens, T. gravida, T. nordenskioldii, Rhizosolenia sertigera, and R. delicatula.

Dinoflagellates. Various dinoflagellates, though seldom as numerically important as the diatoms, are characteristic components of the net plankton. In St. Andrew Bay, Florida, diatoms clearly dominated the phytoplankton (Hopkins 1966). Although little quantitative data were given concerning non-diatom groups, armored dinoflagellates were sparce. Ceratium spp. occurred rarely and silicoflagellates, mainly Dichtoyoca, were sparse.

Patten et. al. (1963) compared the relative abundance of Chesapeake Bay phytoplankton, as determined from net samples, with estimates of relative abundance based on counts of whole water samples. These results show that net collections tend to overemphasize the importance of elongate or colonial diatoms and underestimate the motile, more compact dinoflagellates. No flagellates appeared on the list of important net phytoplankters, whereas when the total phytoplankton was considered, both large flagellates (Peridinium triquetrum, Gymnodinium spp., Massartia rotundata, Prorocentrum triangulatum, Amphidinium fusiforme) and small flagellates (Chilomonas, Cyptomonas sp., Pyramimonas sp.; Dunaliella) were of far greater relative importance. The nanoplankter Chilomonas was actually dominant in numbers, especially during the warmer months.

Perhaps typical of the taxonomic analysis of estuarine phytoplankton is the distribution given by Marshall (1967a) of 74 phytoplankters identified from Willoughby Bay and Hampton Roads, Virginia, 52 were diatoms, 19 were pyrrophytes (dinoflagellates), 1 chlorophyte, 1 euglenophyte, 1 cyanophyte, and 2 cryptophytes. Skeletonema costatum, Asterionella japonica and Nitzschia pungens var. atlantica, were abundant in colder weather while phytoflagellates were present throughout the year but reached peak abundance during the warmer months. A generally similar taxonomic distribution was reported by Kawamura (1962). Of 104 phytoplankton species in Sandy Hook Bay, New Jersey, 60% were diatoms, 22% were dinoflagellates, and 2% cyanophytes.

Nanoplankton. Yentsch and Ryther (1959) suggested that micro-flagellate populations might comprise a significant proportion of the bulk of organic production in marine plankton systems. The basis for this suggestion came from their comparative studies of whole water samples and net samples in which it was shown that many small diatoms (Nitzschia, Thalassiosira, the "summer" form of Skeletonema costatum) and several other species exhibited only about 10% retention in a standard #25 phytoplankton net. Many nano-flagellates (Carteria, Dunaliella, and Gymnodinium) exhibited only 2% retention. Patten et. al. (1963) got two very different pictures of the annual phytoplankton cycle in the lower Chesapeake Bay depending upon whether

net concentrated water samples or whole water samples were used in the taxonomic analyses. In terms of dominance and fidelity, it may well be that certain nanoplankton such as Chilomonas spp. (Patten et. al. 1963, Marshall 1967a, Fournier 1966) or Nannochloris and Stichococcus (Patten 1962b, Ryther 1954) are at least as indicative of a distinctive estuarine plankton community structure as are Acartia and Skeletonema.

Larval stages

In addition to organisms which spend their entire lives as plankton, many crustacea and fish begin their lives as estuarine zooplankton. As these animals grow larger they develop the ability to move against the current. These larger organisms, called "nekton" by ecologists, are the familiar fish and crabs which make up much of man's harvest from the estuaries. It must be remembered that the conspicuous nekton are dependent upon microscopic plankton both for food and because their early stages are planktonic.

Fish Relatively few fish lead an entirely estuarine existance. Killifish (Fundulus majalis) appears to be the most abundant truly estuarine species in the Chesapeake region (McHugh, 1967). Other plankton-feeding herring-like fish move into the middle estuary only during a part of the year. The striped anchovy (Anchoa hepsetus) is abundant in Chesapeake Bay in the summer during which time its eggs are a common constituent of the plankton. Anchovies leave the bay during winter, and their niche in the food web is occupied by the spotted hake (Urophycis regius). A similar seasonal pattern in hake (Urophycis floridanus) abundance has been reported from the Gulf Coast by Gunter (1945).

A variety of fish, several of considerable commercial value, use the middle estuary as a spawning ground or nursery. The hogchoker (Trinectes maculatus), bay anchovy (Anchoa mitchilli) and silver perch (Bairdiella chrysura) are important inshore fish which spawn in Chesapeake Bay (McHugh 1967). Other fish, spot (Leiostomus xanthurus), Atlantic croaker (Micropogon undulatus), and Atlantic menhaden (Brevoortia tyrannus) spawn offshore during colder months. Upon hatching, the young move rapidly into the estuary where they exhibit little growth until the return of warmer weather. Rapid growth occurs in summer as the young fish gradually move down the estuary and into more saline water. At maturity the year-old fish return to the coastal waters and join the breeding stock for future waves of immigrating young. Adults move into the lower estuary in spring but return to shallow offshore waters in the fall. A few fish, such as the wake fish (Cynoscion regalis), spawn in summer. The young spend their first year in offshore waters and then move into the estuary in the following spring.

The great majority of numerically or commercially important estuarine fish thus appear to be only summer residents of the middle estuary. Most explanations of fish migration involve correlations with seasonal "climate" patterns such as temperature, day length, breeding behavior, etc. The relationship of migration patterns to quantity and quality of food sources has not

been sufficiently studied. To what extent are the cyclic changes in structure of producer and consumer levels of the plankton community interrelated and to what extent are they independent of one another (e.g., mutually dependent upon seasonal variations in solar radiation)? Perhaps we do not yet have a sufficient overall grasp of estuarine dynamics to distinguish clearly between cause and effect.

Annual Plankton Periodicity

Chesapeake Bay Winter

The annual phytoplankton cycle of surface waters in the lower Chesapeake Bay has been described by Patten et. al. (1963). Results of taxonomic analyses of whole water samples showed that *Chaetoceros affinis*, *C. compressus*, *C. decipiens*, *Skeletonema costatum*, and *Chilomonas* dominated the winter plankton flora. This community was described as moderately diverse with high redundancy. *S. costatum* was the most significant species in the upper, middle salinity region of the Bay. Environmental conditions during the winter period (December to February) consisted of minimum solar radiation, low water temperature, and instability of the water mass resulting in considerable vertical turbulance. Diatoms dominated the winter flora both with respect to number of individuals and species. The diatom peaks occurred in January and February and resulted primarily from the abundance of *S. costatum*. Winter dominance by this species in coastal waters has been ascribed to its rapid division rate at low temperature and to its requirement for Vitamin B_{12} (Riley 1967a). Burkholder and Burkholder (1956) have demonstrated the presence of Vitamin B_{12} in suspended solids and marsh muds along the Georgia coast, and Droop (1955) has commented on the generally greater availability of vitamins in coastal areas receiving terrestrial runoff.

Spring

With the coming of spring, there was a change-over from a diatom flora to a flagellate flora. Diversity increased such that a clear-cut dominance was not evident. The change-over began in the upper bay and was characterized by different species being dominant at various stations. *Ceratulina bergonii* was the major spring diatom and was dominant at some stations while the flagellates *Peridinium triquetrum*, *Massartia rotundata*, and *Chilomonas* sp. were variously dominant at others. Additional spring phytoplankton of slightly lesser importance were the flagellates *Cryptomonas* sp., *Gymnodinium* sp., and the diatoms *Asterionella japonica*, *Chaetoceros affinis*, *C. compressus*, *C. gracilis*, and *Leptocylindrus danicus*. Environmental changes associated with the change in flora included lengthening warmer days, a decrease in organic seston load and absorbed orthophosphate, and an increase in organic phosphate.

Summer

With the approach of summer, the flagellates moved to a position of even greater floristic importance. Community redundancy remained low and

there were no particular dominants although cell concentrations were greatest toward the upper reaches of the estuary. Components of the summer phytoplankton flora, in order of decreasing numerical importance, were Chilomonas sp., Massartia rotundata, Pryamimonas sp., Cryptomonas sp., Skeletonoma costatum and Amphidinium fusiforme. Skeletonema increased in relative importance toward the end of summer (August). The summer environment was characterized as a period of maximum solar radiation and greatest vertical stability in the water mass. Patten et. al (1963) suggested that perhaps regeneration of the defunct winter and spring floras, beginning toward the end of summer, was casually related to an observed gradual increase in orthophosphate during the warm months.

Fall

During autumn Skeletonema completed its return to ascendency although total population level was low. Microflagellates dominated numerically throughout most of the period. The flora, in order of decreasing numerical importance. consisted of Chilomonas sp., Dunaliella sp., Massartia rotundata, Prorocentrum triangulatum, Skeletonema costatum and Pyramimonas sp. Redundancy was low. The flagellates exhibited a short second peak in October-November, and it was suggested that this may have been causally related to an orthophosphate as a result of increased terrestrial runoff and destruction of stratification.

Patten (1963c) has gone a step further than most students of estuarine phytoplankton. He has described the annual periodicity of plankton taxa and noted correlations with environmental variables; but, in addition, he has attempted to interpret these in terms of energy flow and conservation of energy. When viewed in this manner, the alternation of flagellate (summer) and diatom (winter) floras becomes community response to changing biotope in such a way as to maximize biomass and stability. Patten has drawn an analogy between conservation of energy by the plankton community and cost-profit principles of economics. He has suggested that the "community appears capable of a strategy of speculation in persuing the objective of maximizing its biomass. . . (and) its stability in variable environment." Thus, in summer efficient management depends upon plankters having high light optima, rapid dynamics, short generation time, and motility. In winter the advantage shifts to forms having lower light optima, longer generation time, greater capacity for food storage, and structural features which take advantage of water movements as a means of remaining suspended.

Other Locations

Perhaps the most extensive series of consecutive observations of estuarine phytoplankton is that reported by Riley and Conover (1967) for Long Island Sound. Although a broadly consistent seasonal cycle was observed, it was characterized by year-to-year variations. In general, six floristic phases were recognized as constituting the annual phytoplankton cycle.

The diatoms Thalassiosira decipiens and Paralia sulcata dominated a midwinter flora characterized by a paucity of individuals. Skeletonema

costatum was the major constituent of periodic "flowerings" during late winter while Thalassionema nitzschioides advanced from a position of minor importance to second rank.

A flowering period (March-April) seemed to represent a transition from a situation of moderate diversity and a uniform dominance to one of reduced total population, less species diversity, and patchy dominance. Leptocylindrus sp. and Rhizosolenia delicatula were usually present together, but from year to year varied with respect to relative importance. Chaetoceros dubile, Schroderella delicatula, and Peridinium trochoideum became major phytoplankton constituents, but no single species was dominant at all stations.

Blooms of Skeletonema costatum dominated during early summer with considerable year-to-year variation in associate species. The summer period (July-August) was characterized by small to moderate populations with no overwhelming dominance. The summer flora consisted about equally of diatoms and dinoflagellates, species of Skeletonema, Thasassionema, Exuviella, Peridinium, and Prorcentrum being of greatest importance.

Riley and Conover (1967) concluded that light and temperature were the major environmental variables which influenced and seasonal periodicity of phytoplankton in Long Island Sound. Salinity was of less importance while nitrogen was usually the most important limiting factor. Chemical interaction (stimulation or inhibition) among phytoplankton species was suggested as a factor of possible importance in determining the course of seasonal periodicity.

Summation

If there is a system-wide pattern of estuarine phytoplankton periodicity, it would seem to consist of repeating seasonal variations in the relative abundance of its three principal components: diatoms, dinoflagellates, and nanoplankton (often nanoflagellates). In general, diatoms dominate the winter flora, but share or yield dominance to dinoflagellates during the summer. Nanoflagellates are usually present throughout the year, but may exhibit spring or fall blooms (Marshall 1967a).

Patten (1963c)has pointed out that seasonal alterations in the structure of a phytoplankton community may occur as a result of: 1) differential reproduction and selective elimination of component species, and 2) water mass transfer and consequent dispersal or concentration. The resultant diversity changes, usually cyclic over many years, give in a single year, the appearance of ecological succession. The significance of diversity can be illustrated by conclusions drawn by Patten (1962b) with respect to his study of species diversity in Raritan Bay. Higher diversity levels prevailed in the lower estuary, signifying higher biotype quality (greater variety in ecological niches) toward lower bay. Progressive diminution of diversity upbay was thought to indicate a more unsatisfactory biotope (reduced number of niches resulting from gross pollution originating at the head of the estuary).

Vertical Distribution

Many studies of plankton periodicity have been based on surface or near-surface samples. Patten (1963) reported that Skeletonema costatum was ten times more abundant near the bottom of the York River than in the upper ten feet. Similarly Massartia and Chilomonas were dominant at the surface, Gyrodinium was dominant at six feet while Eutreptia, Pyramimonas, and Leptocylindrus (species not represented at all at the surface) were dominant at ten feet. Studies of photosynthetic maxima suggested that populations down to compensation depth (mean 6.5') were geared for production at low efficiency and high power output, while those in the tropholytic zone beneath operated at somewhat higher efficiencies but with reduced energy throughout. Adaptation to a particular level was thought to involve physiological factors such as photoinhibition and ecological factors. Comparison of the extent of vertical stratification with various hydrographic variables suggested that intensity of stratification was in excess of that attributable to the corresponding level of heterogeneity of the physical environment . Maintenance of such a concentration gradient against the mixing forces of the water mass was therefore considered to be endergonic. It was concluded that the organisms must expend biomass energy in order to reduce the entropy of their distribution in space.

Patten (1963) used his economics analogy (marginal utility theory) of plankton production to explain vertical distribution patterns. Light energy decreases with depths so that cost of production must increase as depth increases. The phytoplankton community must expend energy to concentrate its component organisms near the surface up to the point of decreasing return on the investment. If marginal utility is negative, the scale of activity should be reduced until no further net loss is incurred. For the whole community to achieve net positive balance in the water column, energy losses in the zone beneath compensation depth should be kept minimal. In natural situations this may be achieved by increasing photosynthetic capacity or decreasing respiratory rate (or both) with depth.

Since settling of the phytoplankton is a function of metabolic vigor and energy intake, the loss of old and feeble individuals from the phototropic zone is viewed as a biocoenose deriving a utility advantage through removal of biomass which has ceased to be productive.

A physiological explanation of dim light "adaptation" by algae has been presented by Yentsch and Lee (1966). Using cultures of the nanoplankter Nannochloris atomus, they concluded that the explanation of "sun" and "shade" phytoplankton lay in the inability of algae to maintain a high level of dark reaction enzymes under very weak light conditions. Upon the return of adequate light so few enzyme molecules remain that photosynthetic light saturation occurs at even very low intensities.

Lower photosynthetic rate at increasing depths is thus interpreted as resulting from phytoplankton that are not physiologically "up-to-par." Support for this conclusion was derived fromobservations that products of

chloroplast decomposition frequently occur in algal cells recovered from the base of the euphotic zone. Chlorophyll content of any particular cell is a function of the relative rates of pigment synthesis and pigment destruction. Pigment destruction may occur during periods of weak light intensity or by photooxidation at high light intensity.

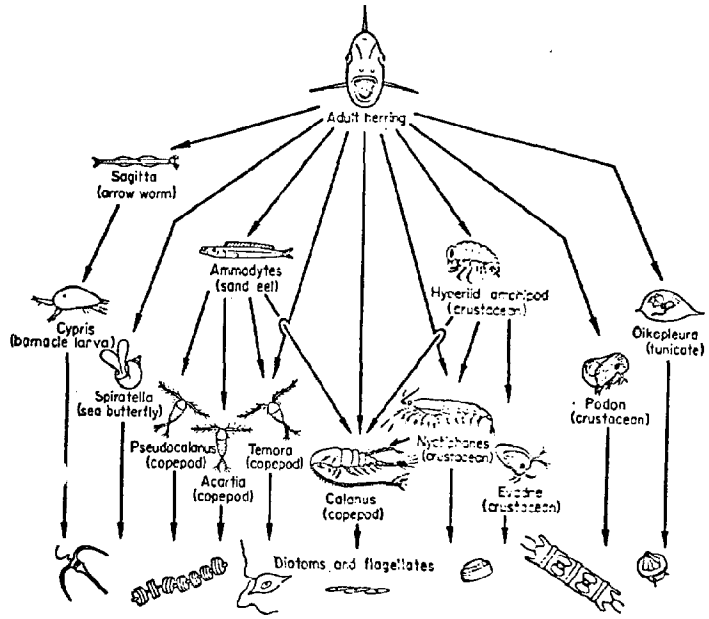
System Dynamics

Plankton organisms form the dominant biomass of the middle estuary and thus constitute the base of its food web. Photosynthetic production by the phytoplankton serves as a direct source of biotrophic energy inflow. Invisible diatoms and phytoflagellates are the primary food of just visible copepods which in turn are eaten by relatively small herring-like fish. Figure 20 represents the sort of complex web that can develop when food chains are integrated at the genus level. This diagram shows that economically important, readily visible, estuarine fish are ultimately, although indirectly, dependent upon invisible components of the system. Many, many microscopic, usually shortlived, producers must be eaten in order to support many times fewer, longer lived, consumers. Stability of the upper levels of consumption (herring) may be achieved by the consumer by changing feeding rate, metabolic rate, or by shifting feeding habits. Seasonal changes in the relative abundance of plankton producers may result in a shift in relative abundance among lower level consumers (various copepods, etc.). Thus different branches of the food web may become relatively more important at some seasons than at others.

Herring, anchovies, smelt, and minnows in their turn serve as food for still larger fish. Figure 21 shows the food relationships of the carniverous striped bass. Note that, with the exception of a box labeled "Algae" at the lower left, only various levels of consumers are shown in this web. It is evident from this diagram that such economically unattractive animals as gobies and jelly-fish (coelenterates) as well as the almost invisible plankters (cladocera and copepods) may be important links in food chains ending with fish species of commercial importance. Fig. 22 is a simplified version.

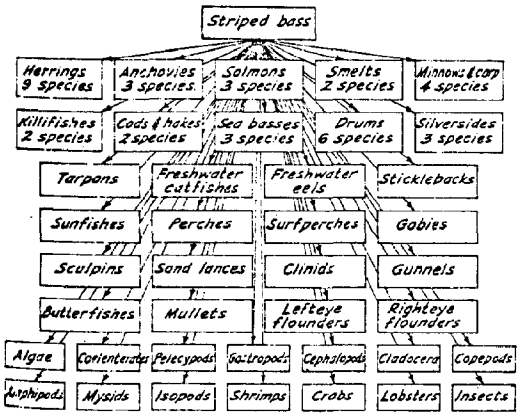
A less obvious, but under some condition equally significant, energy input derives from import into the system of dissolved and particulate organic matter. At least in some estuaries, estimates of production capacity based on phytoplankton studies may be conservative because of failure to consider the availability of organic energy sources.

Regular seasonal patterns of plankton distribution and the ratio of autotrophs to heterotrophs suggest the presence of an annual program of successive intergrading patterns in systemtrophic structure. The annual pattern of surface phytoplankton production, exclusive of the nanoplankton, in the lower Chesapeake Bay was indicated by periodic measures of total chlorophyll (Patten et. al. 1963). Total chlorophyll ranged from 0.94 - 22.27ug/l and averaged about 5 - 7ug/l. Highest chlorophyll concentrations were observed near the mouth of the York River in the spring (April) and corresponded to plankton counts averaging 1600-2200 units/ml (max. 6380 units/ml). Chlorophyll

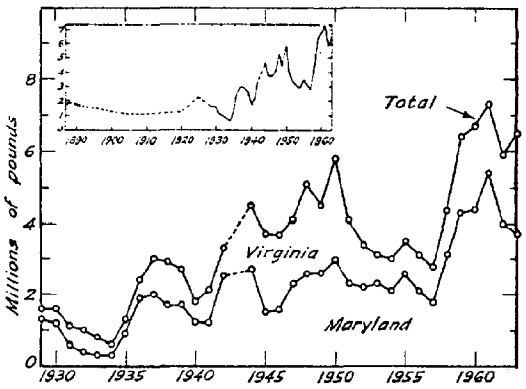


The feeding relationships of adult herring. (Based on HARDY, 1924 and 1959; courtesy of Collins.)

Fig. 20. Food chains of herring-like fishes. This example is from Europe and involves some feeding outside of the middle salinity zones.

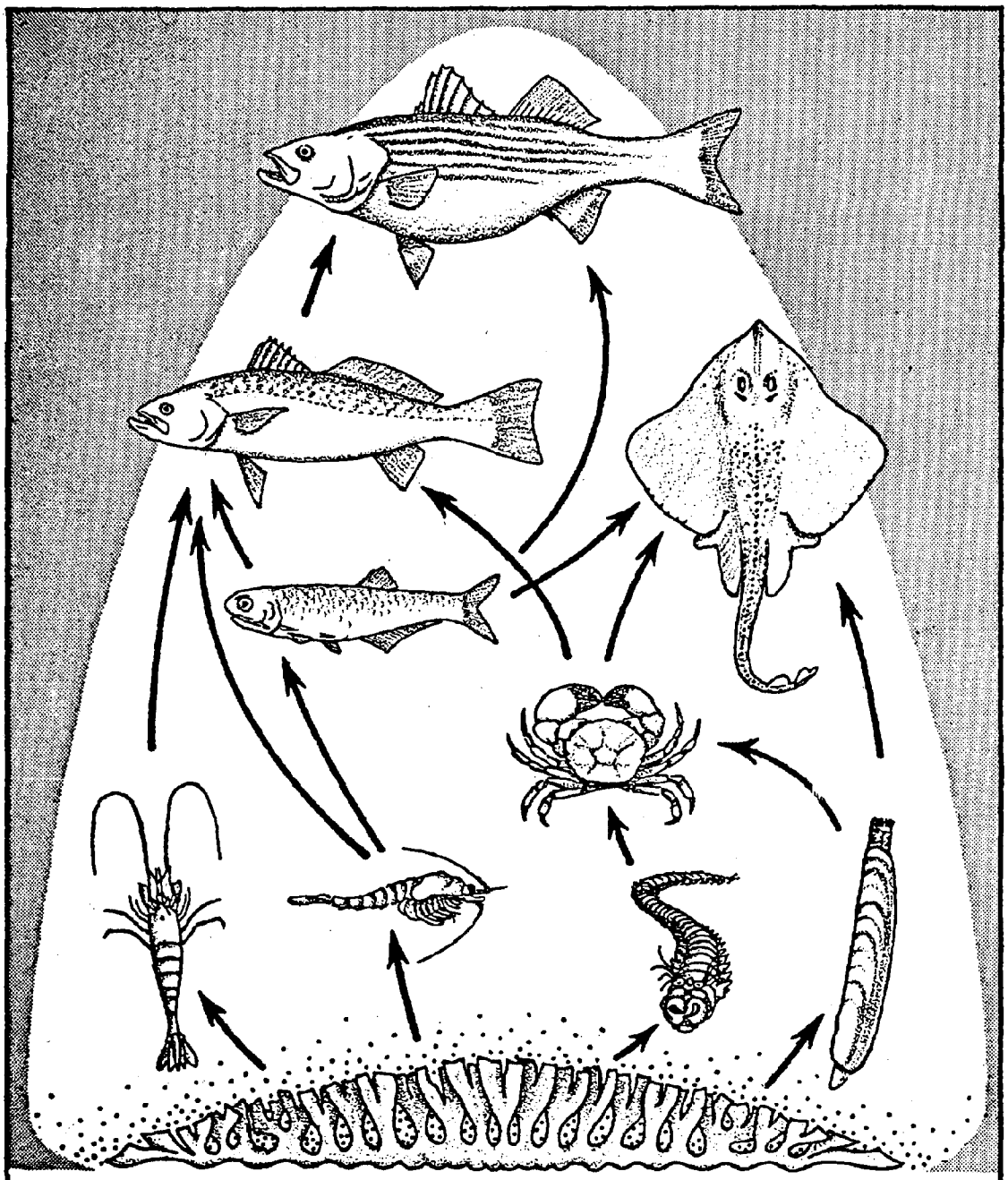


Simplified diagram of the food relationships of striped bass (*Roccus saxatilis*). Data from Raney (1952) and Hollis (1952).



Commercial catches of striped bass (*Roccus saxatilis*) in the Chesapeake Bay states since 1929. Inset shows the recorded catch of striped bass in Chesapeake Bay since 1887.

Fig. 21. Food chain and catch of striped bass (McHugh, 1967).



A SIMPLIFIED FOOD WEB ILLUSTRATING SOME OF THE PATHWAYS OF FOOD IN THE FOOD PYRAMID INVOLVING THE WEAKFISH. THE ARROWS POINT TO THE CONSUMERS. THE INSERT (RIGHT) IDENTIFIES EACH ORGANISM. (MODIFIED FROM DAIBER, 1959)

A BIOLOGICAL EVALUATION OF
THE DELAWARE RIVER ESTUARY
UNIVERSITY OF DELAWARE MARINE LABORATORIES

STRIPED BASS

WEAKFISH SKATE

ANCHOVY

MUD CRAB

GLASS SHRIMP MYSID SHRIMP CLAM WORM RAZOR CLAM

ORGANIC DETRITUS AND PLANT LIFE

Fig. 22. Food Web (Shuster, 1959).

concentration was consistently greatest near river mouths at the head of the estuary and gradually diminished toward the ocean. Cell counts were generally higher on the western side of the estuary than on the eastern, more saline side. The overall chlorophyll pattern consisted of a spring maximum with lesser peaks in the fall. Chlorophyll minima were recorded in July and January.

Hopkins (1966) found that diatoms and copepods dominated the plankton of St. Andrew Bay. An attempt to analyze the interdependence between the important producers and consumers revealed that diatom biomass accounted for a significant portion of zooplankton biomass variance (11.5%), but that at best, 20% of the diatom biomass variability could be attributed to the combined effects of salinity and temperature. It was concluded that only a small portion of the total variance of zooplankton biomass can be accounted for by temperature, salinity, and diatom biomass together. In St. Andrew Bay the diatom (phytoplankton) concentration was always greatest in medium salinity water, although greatest diatom diversity was associated with more saline water. Average number of diatomsper liter for the entire bay was 8×10^5 with peaks occurring in late summer (August), winter (February) and spring (May). Peaks in packed cell volume per liter were observed in November and June with minima in April and September, and thus were not correlated with cell numbers.

Phytoplankton-zooplankton relationships in Narragansett Bay have been given rather detailed attention by Martin (1965, 1968). Skeletonema costatum was the dominant phytoplankter except in autumn when it was replaced by Rhizosolenia delicatula. Principal grazers were Acartia clausi in winter and spring and Acartia tonsa in summer and autumn. Skeletonema costatum, and other phytoplankters, may exist in a variety of physiological states such that estimates of production output per individual vary with the "stage of development" in the annual cycle. Patten and Van Dyne (1968) showed that computed values of gross production and respiration for S. costatum were positively correlated in the York River plankton such that early summer populations exhibited low estimated average gross production, but increased to high levels in mid-July followed by a decline to minimal levels in late July. Maximum values were again observed in August. These results suggested that S. costatum is a bloom form with quiescent stages which prevail in the benthos during periods of inactivity. Many widely distributed phytoplankton diatoms appear to exist as ecological races. Clones of S. costatum, Asterionella japonica, Chaetoceros didymus, and others isolated from South American waters were unable to grow at low temperatures, whereas clones of the same species isolated from waters off Cape Cod grew well down to 3-4C (Hulburt and Guillard, 1968).

Morphologically, and possibly physiologically, distinctive summer and winter forms have also been reported for oceanic plankton diatoms (Chaetoceros decipiens) (Raymont 1963b).

Martin (1968) related the annual pattern of relative abundance within Narragansett Bay, a system dominated by Skeletonema-Acartia, to seasonal variations in the physiological condition of diatom producers and copepod consumers. It is generally assumed that nitrogen and phosphorus concentrations

are among the more important factors involved in phytoplankton production. Martin (1968) showed that glucose comprised 27% of the organics in S. costatum during the spring in Narragansett Bay. Zooplankton (Acartia clausi) oxidized about 23% of the ingested organic matter. Thus carbohydrates alone could account for the entire zooplankton metabolic requirement. During the spring phytoplankton grazing zooplankters readily convert carbohydrates to cellular energy but store lipids and proteins. Available nitrogen and phosphorus are thus depleted. As the season progresses, phytoplankton metabolism gradually shifts from carbohydrate storage to lipid storage. Generally this is accompanied by a decrease in reproductive rate and the appearance of intracellular oil droplets. Such cells are described by Martin (1968) as senescent. Zooplankter grazers cannot now obtain their nutritional requirements solely from the now reduced supply of phytoplankton carbohydrate and must expend more respiratory energy in oxidizing lipid. A physiologically more efficient process (requiring less cellular energy input) would be the deamination of stored proteins thus freeing organic acids for carbohydrate oxidation. Respiratory breakdown of stored zooplankton lipids (apparently reservoirs for phosphate) results in their conversion to carbohydrates and subsequent release of phosphorus. Excretory release of stored nitrogen and phosphorus may now stimulate another phytoplankton peak. Martin (1968) supported this explanation of alternating zooplankton excretion rates in Narragansett Bay. Spring excretion rates averaged 0.25 μg at. N/mg dry wt.-day and 0.078 μg at. P/mg dry wt.-day while comparable fall values increased to 2.42 μg. at. N/mg dry wt.-day and 0.215 μg. at. P/mg dry wt.-day.

Patten and Chabot (1966) have criticized productivity estimates based solely on cell abundance and species composition on the grounds that such information does not take into account temporal or spatial differences in the physiological state of populations under study. They point out that the energy dynamics involving nutritional and physiological states of component populations depends upon interaction with one another and with the ambient environment. Estimates of productivity must be based upon species composition data properly weighted for physiological state (biologically useful energy content).

The relationship of nutrient availability to phytoplankton production was demonstrated by Fournier (1966). Water samples from the York River were enriched with various nutrients. Nitrate, phosphate, and all or part of the trace metals generally limited production only in a negative sense when present in excessive amounts or from some unexplained factor in the enrichment itself. It was further noted that the same community might show sensitivity to another set of limiting factors if it were at some other physiological stage.

Earlier studies in Narragansett Bay (Smayda 1957) suggested that the winter-spring diatom flowering resulted from release of zooplankton grazing pressure. Amplitude of the diatom peak was correlated to the length of the optimal growth season and the availability of silicate. Growth of diatoms was reported after nitrate depletion but never after silicate depletion (Pratt 1965).

More subtle energy exchanges have been documented; but in most cases, their quantitative significance and uniformity of occurrence are poorly understood. For instance, Altschuler and Riley (1967) found that the number of Flavobacterium and other bacteria in the surface waters of Long Island Sound was one order of magnitude (average 8370/ml) greater than that of the phytoplankton and organic aggregates. Maximum counts were recorded during warm weather and minima during winter. It was suggested that these bacteria were probably free-living or attached to suspended silt or particulate aggregates. The significance of these bacteria is probably related to their common occurrence on the surface of particulate organic matter. Such substances may thus be reduced to a simpler soluble form. By this means, heterotrophic and auxotrophic plankters may be placed in a more favorable nutritional environment and the turnover rate of carbon and other nutrients speeded up.

A number of estuarine algae have been found to excrete 7-16% of their photo-assimilated carbon. Glycollic acid formed 9-38% of this material in S. costatum and several other phytoplankters both in culture and in water samples from Vinyard Sound and the Gulf of Mexico (Hellebust 1965). Other substances excreted by algae included proline, glycerol, and mannitol. The type and rate of substance excreted varied with the physiological state of the population. For instance, the greatest excretion of glycollic acid by S. costatum occurred when light was limiting. The released carbon was not reassimilated by S. costatum but was taken up in considerable quantities by Cyclotella nana; C. nana was found to excrete negligible amounts of glycollic acid. Unfortunately, the nutritional characteristics of most estuarine phytoplankters are unknown as is their capacity for excretion. The significance of algal excretion to annual patterns of relative plankton abundance thus remains unknown.

Although carbon dioxide fixation is normally associated only with plants, evidence is accumulating that photosynthetic assimilation is supplemented by carbon dioxide fixation in many marine animals. Hammen (1964) reviewed the literature dealing with carbon dioxide fixation in marine invertebrates. In all some twenty species representing fourteen phyla (including sponges, worms, starfish, mollusks, and arthropods) have been shown to fix carbon dioxide. The most probable metabolic pathway for this form of assimilation seems to be carboxylation of organic acids, particularly propionate to succinate and pyruvate to malate. Quantitative studies of carboxylative fixation of carbon dioxide in natural systems has not been undertaken; but consideration of the wide range of animal phyla involved, together with the fact that these animals frequently constitute an important fraction of the biomass in estuarine environments, suggest that this metabolic route may contribute significantly to primary production.

On land, fungal parasites often decimate entire populations and thus affect population densities. A number of marine phytoplankters (diatoms and dinoflagellates) are parasitized by chytridiomycetes and oomycetes (Johnson 1966a). Epidemics are rare or infrequently reported; but such a possibility should not be discounted, especially when unusual and dramatic changes occur in established patterns.

Moving water constitutes a force capable of doing work. Currents and the water masses which comprise them carry suspended organic and inorganic substances. Dissolved substances may become colloidal particles as they progress along a density-alkalinity gradient. This suspended load is important as a potential source of nutrients, in providing both a substrate and surface area for bacterial and fungal growth, as a direct source of food for filter feeders, and because its density affects water turbidity and thus the capacity for photosynthetic conversion of light energy.

In the lower York River the total concentration of suspended material was found to increase with depth (Patten, Young, and Roberts 1966). Organic matter showed a uniform vertical distribution. It was concluded that the difference in vertical distribution resulted primarily from the inorganic component. The average time taken for material to settle from two feet to twenty-two feet was 0.13 days for total suspended matter, 0.34 days for organic, and 0.06 for inorganic. Distribution patterns of mineral grains suspended in the Chesapeake Bay have been described by Bond and Meade (1966) who reported that the (inorganic) suspended sediment seemed to be derived from local sources. No general correlation was observed between vertical suspended matter distributions and those of phytoplankton populations or between size of populations and concentrations of particles; however, the concentration of organic matter was higher and that of inorganic matter lower during the period of reduced phytoplankton following the spring bloom.

Suspended organic matter may arise from: (1) detritus derived from normal biotic components of the water column, (2) import from upstream or the edge, (3) resuspension from the bottom resulting from upwellings and eddys or, (4) formation and aggregation of colloidal particles. Regardless of its manner or formation, such material is generally called 'detritus'. Quantitative information concerning the relative importance of the various sources is lacking although the magnitude of non-living particulate material, relative to the phytoplankton concentration, is such that it constitutes a resource of potentially major significance in the trophic economy of inshore waters (Patten, Young, Roberts 1966).

Moving water masses interact with the bottom in such a way that sediments are frequently picked up and redeposited elsewhere. Interaction between these sediments and their medium during transport results in mineral and nutrient exchanges. Large pieces of organic matter settle to the bottom and there become reduced to a smaller, more soluble, or colloidal, state. Resuspension of this material would result in dispersal and increased surface contact with water. Since the organic components settle more slowly than the inorganics, water movement has performed work in bringing about a sorting process and the water phase becomes richer in dissolved and particulate organics. This change in chemical status may be further complicated in some environments or at certain seasons by the transfer of materials from a reducing environment on the bottom to an oxidizing one above.

At least under some conditions phytoplankton production may be insignificant when compared to that from other sources. Ragotski (1959) demonstrated that, while average gross phytoplankton production amounted to 0.68 $gC/m^2/day$,

average net phytoplankton was -0.038gC/m^2/day. This plankton community was heterotrophic in summer and autotrophic only during winter. The surrounding salt marsh was postulated as the outside source of organic matter entering this system. Low phytoplankton efficiency was related to poor light penetration due to conditions of high turbidity.

In shallow estuaries where benthic production outstrips phytoplankton production, bottom living animals may contribute more to the herbivore links in the food chain than zooplankton. Thus is shallow sounds in the vicinity of Morehead City, North Carolina, Williams et. al. (1968) found that waters dominated by Acartia tonsa and Skeletonema costatum was characterized by low zooplankton density. It was suggested that the phytoplankton-zooplankton links in marine food chains may be of greatest importance in waters deeper than 100 meters, but become steadily less important with decreasing depth in areas shallower than 100 meters. Phytoplankton net production (53g carbon/m^2/year) was comparable to that of the open sea, but was concentrated vertically in the upper 1.2 meter layer. In small estuaries of the type described here, the major contribution of the phytoplankton would seem to come after it settles to the bottom.

Larval and post-larval forms of numerous fish and crustacea, many of commercial importance, contribute to the total plankton biomass. Depending upon the life history of the species involved, these 'meroplankton' may constitute a significant proportion of the primary and secondary consumers in the plankton system.

The distribution of bothid flounder (Paralichthys dentatus, P. lethostigma) and penaeid shrimp (Penaeus aztecus, P. duodarum) post-larvae in the North Carolina sounds was followed over a ten-year period by Williams and Deubler (1968b). They observed that the greatest density of both genera occurred near inlets. Analysis of distribution patterns and environmental variables led to the suggestion that varying conditions of light present during new and full-moon periods may be a causal factor in sample-size differences observed.

Geographical Variations

The middle estuary may be typified by certain universal characteristics, including a plankton based food web and relatively well mixed brackish water. Herring-like fish harvest the plankton and are in turn harvested by larger fish or man. The general physical characteristics of the middle estuary are similar; yet geographically separated estuaries may present very different species lists. Closer analysis reveals that, while the names of the actors may be different, the play, the plot, and the characters are the same. For instance, the herring (Clupea harengus) plays the part of an efficient plankton gatherer in deep cold estuaries of Maine, while in shallow warm estuaries of North Carolina this position in the food web is dominated by menhaden (Brevoortia tyrannus). Ecologists refer to this sort of "role playing" as niche substitution. Thus similar positions on a generalized "middle estuary food web" are occupied by functionally, and often morphologically, similar forms. The actual species

present in any particular estuary depends upon environmental factors affecting the distribution of organisms. The middle estuary therefore has a variety of biotic expressions which seem to show broad correlations with climate and geography.

Along the New England coast of the United States, the middle estuary is most extensive in the open water inside the front line of islands of Maine, Other northeastern examples of this system are: middle portions of the Merrimack river in Massachusetts, lower Narragansett Bay in Rhode Island, and Long Island Sound in New York.

Plankton studies of Sheepscot Bay and other Maine estuaries (Stickney 1959; Sherman 1963, 1966a, 1966b, 1968) show that the food web rests on a typical phytoplankton-copepod base. Acartia and Pseudocalanus are the primary food supporting populations of herring larvae (Clupea harengus) (Graham and Venno 1968, Sherman and Honey 1968). Nekton components of this system are the lobster (Homarus) (Sherman and Lewis 1967, Scattergood 1960a) and a migratory shrimp (Pandalus). Alewives and various salmonoid fish are important summer residents. More southerly estuaries in New England are generally comparable to those of Maine except that tidal amplitude is less and circulation more gentle. Narragansett Bay and similar estuaries tend to be more protected and shallower than more northerly estuaries. These estuaries are also much closer to centers of human population and thus more subject to modification by a variety of man-made influences such as domestic waste, industrial effluent ranging from heavy metal poisons to pulp mill and textile chemicals, and development activities including siltation from construction or removal of substrate by dredging.

New York estuaries generally show various stages of pollution. Ryther's studies of Moriches Bay have become classics in estuarine ecology. New Yorkers were given an object lesson in basic ecology when they discovered that the price of fresh duck was near decimation of the Long Island Sound oyster fishery. Long Island farmers imported corn and other protein-rich grains as food for their ducks. Some of this protein became incorporated into valuable duck meat while the rest was lost as nitrogen-rich duck excretia. Subsequent release of this nitrogen through decomposition of the excretia resulted in a marked increase in soluble nitrogen in streams leading into Long Island Sound. Nitrogen happened to be a nutrient of limiting importance to the phytoplankton. Increased nitrogen was accompanied by greater phytoplankton production, but less desirable nanoplankton (Nannochloris and Stichococcus). Thus balance within the food web was upset with most of the increase in total biomass resulting from only a few food pathways and to the detriment of the oyster fishery. Duck farmers are now controlling their nitrogen losses but a host of new problems has arisen which prevent the estuaries from achieving something

of their previous balance. Dredging and filling operations continue while marsh draining, thermal addition, pesticides, and oil spills may be expected to increase rapidly in the near future. The biota of Long Island Sound may change to such a degree that it no longer fits the description of a medium salinity system. Instead it may evolve irreversibly into a new system better suited for the role of tertiary sewage treatment.

Chesapeake Bay is the largest estuary between New York and North Carolina. Details concerning the medium salinity plankton-based portion of this estuary have already been given. Principal differences between the Chesapeake and more northern estuaries include more gentle circulation in the Chesapeake and differences in dominant biota. Lobster and herring are no longer dominant nekton, being replaced by more southerly species such as bluefish, striped bass, flounder, mullet, blue-crab, and shad. Portions of this system may have a bottom dominated by Mya or oyster reef complexes. Other estuaries having characteristics similar to Chesapeake Bay are Raritan Bay in New Jersey and Delaware Bay.

The markedly different oceanic biotas north and south of Cape Hatteras are not reflected in coastal systems behind the barrier islands. Shape and depth constitute the primary differences between Chesapeake Bay and the North Carolina Sounds. Shallow depth and dampened tidal effects promote good mixing. Water masses tend to be relatively turbid and move about in broad gentle swirls rather than as part of a current. Patterns of water movement depend in large measure on wind direction and velocity. In reality, the sounds are shallow basins into which the estuaries empty. Lower levels of the food web in these sounds have been incompletely studied. In general, production is accomplished by diatoms and dinoflagellates. This energy moves up to the nekton level via copepods. Thus the overall play is similar to that occurring in Maine estuaries but the names of the actors are different. Dominant nekton are of the characteristic "southern" types (e.g. bluefish, striped bass, flounder, mullet, and shad). Blue-crab (Callinectes) and menhaden (Brevoortia) are abundant and of considerable economic importance.

North Carolina's sounds constitute the largest estuarine system along the Atlantic coast. Most of this vast system is of the medium salinity, plankton-based type and as such functions as a nursery or a temporary home for migrating nekton of commercial importance. Shrimp, striped bass, and menhaden do most of their "growing" during periods spent in the sounds or near shore coastal waters where they become the beneficiaries of a high level of phytoplankton production. In estuarine systems such as this, efficiency of energy transfer between plant and animal is greater than in most land environments. This is so because the producer components of the food web are primarily diatoms. Diatoms convert some of their carbon intake to energy-rich (high calorie) fats and oils while most green plants store carbon as less rich carbohydrates. In practical terms this means that a mouthful of diatoms is more valuable to a fish than a mouthful of Nanochloris or other green algae. In fact, the oil which makes menhaden of commercial importance is produced by diatoms and then stored and concentrated by various fish as it moves along the food chain to menhaden.

Large size, isolation, and low human populations in the region have stalled industrial development such that the Pamlico and its sister estuaries remain among the least polluted and potentially most valuable along the east coast. The interrelationships between marsh, open water, inflowing rivers, and fisheries production are becoming evident to a few, but many people cannot see any possible connection between "swamp drainage" and figures relating to the commercial catch of shrimp. This level of understanding of the estuarine system together with public demand for recreational and industrial development suggest that the North Carolina sounds may be in for a real test of their capacity to absorb shock without deleterious, irreversible changes occurring. Currently shock is being generated by dredging and filling operations designed to stabilize land for beach development, by changing patterns in runoff as a result of impoundments on tributary rivers, and by destruction of the marsh through ditching and draining projects.

Agricultural land adjacent to rivers leading into the sounds provides significant amounts of pesticides to estuarine food cycles. Only a few cases have been documented in which fish kills or other less obvious deleterious effects have resulted from use of pesticides. Although impressive biotic changes result from massive accidental influxes of pesticides, less dramatic, but subtle and potentially more significant biotic changes may be induced by long term gradual build-up of pesticide accumulation as foods move up through the food web.

Large scale phosphate mining adjacent to the sounds might be expected to alter the chemical characteristics of the estuary. Current studies suggest that nitrogen is also an important limiting factor. It seems likely that development of the phosphate resource will stimulate a trend toward greater industrialization of the area, more employment, and a larger financial base for local political structures. The ultimate effect of these changes is greater population. As sewage wastes mount, shellfish areas become contaminated and must be closed. Continued addition of nitrogen-rich sewage together with the already increased phosphate content of the water may produce explosive blooms of nanoplankton such as occur in polluted estuaries further north. Thus although total plant production would be increased, the new dominant forms may not be of a type capable of supporting the present nekton fauna. Evolution of a new production base will probably result in other shifts further up the food web. The New York experience indicates that such changes are seldom desirable.

Less widespread factors tending to upset local portions of the estuary include wastes from menhaden and other fish processing plants, brine pollution from an experimental desalination plant and from attempts to eliminate certain fresh-water aquatic weeds by pumping in salt water until their salinity tolerance is exceeded.

South of Cape Fear, rivers such as the Pee Dee in South Carolina and the Savannah in Georgia empty into the sea via low marshland. Extension barrier islands, of the type responsible for formation of the North Carolina Sounds, are absent or much reduced in importance. Consequently, estuaries along this portion of the Atlantic Coast have been described as a "muddy river mouth" type. Here the "middle-salinity-plankton-based" system consists of tidal channels through the salt marsh, major portions of the Charleston and Georgetown harbors, and a ten to twelve mile wide strip of "estuarine" water which remains trapped between higher salinity ocean water and the beach. Sport fisheries, dependent at least in part on the middle estuary plankton, are similar to those of the North Carolina sounds. Commercial fisheries involve primarily oysters and blue crabs, both of which are directly dependent upon the plankton during one or more stages in their life cycle. Shrimp become of increasing commercial importance southward along the Georgia coast.

Among the commercially important components of the middle estuary system, herring and lobster ride at the head of the plankton-based food web in New England. This dominance shifts to shellfish and a polluted system in New York which merges with the shellfish, blue-crab fishery of the Chesapeake Bay. Menhaden, shellfish, blue-crab, and to a lesser degree shrimp, are important in North Carolina. The shrimp fishery increases in importance southward from North Carolina, but reaches its peak along the Gulf Coast.

Chapter C-10

STRATIFIED ESTUARIES

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INTRODUCTION

This chapter will be devoted to stratified estuaries that are sometimes stagnant. Their vertical circulation is limited by their density stratification and their horizontal circulation is limited by their geomorphology. Many, but not all of these systems are fjords.

In such waters of restricted circulation, a density stratification develops because of the non-uniform vertical distribution of heat and salt content. The upper zone is aerated and supports phytoplankton photosynthesis, whereas organic matter decomposes in the lower zones, which become anoxic and develop characteristic chemical properties and ultimately produce hydrogen sulfide. There is a cycle of minerals in these systems that may support a rich biota in the upper layers. The anoxic bottoms sustain only bacteria, and organic matter accumulates in the undisturbed sediments. In stratified estuaries subject to large seasonal variations in sediment input or to alternating oxidizing and reducing conditions on the bottom, the sediments form in banded layers called varves. In addition to natural stratified systems, the dispersal of wastes into waters of restricted circulation may artificially produce stratified systems with anoxic hypolimnetic bottom zones. Dredged channels may also stratify, become anoxic, and develop hydrogen sulfide.

EXAMPLES

Ecological and other studies have been made in representative examples of stratified estuaries. The examples include natural systems, system altered by the introduction of wastes, a dredged system, and examples from tropical and northern waters. Many of the systems in northern waters are typical fjords.

Stratified Natural Fjords

An example of these systems is Deep Inlet, Baranoff, Alaska (Figs. 1, 2, 3), an estuary that was studied by Andersen (1962). It is about 7.5 km long, 0.9 km wide, and relatively deep, 102 m, with a mouth that is horizontally restricted and has a sill depth of 26 m. In September 1960, the near bottom water was nearly devoid of dissolved oxygen and contained large concentrations of inorganic phosphate (Fig. 2). At the time of the observations, there was a fairly weak pycnocline between 25 and 50 m (the observations were not vertically close enough to define the pycnocline

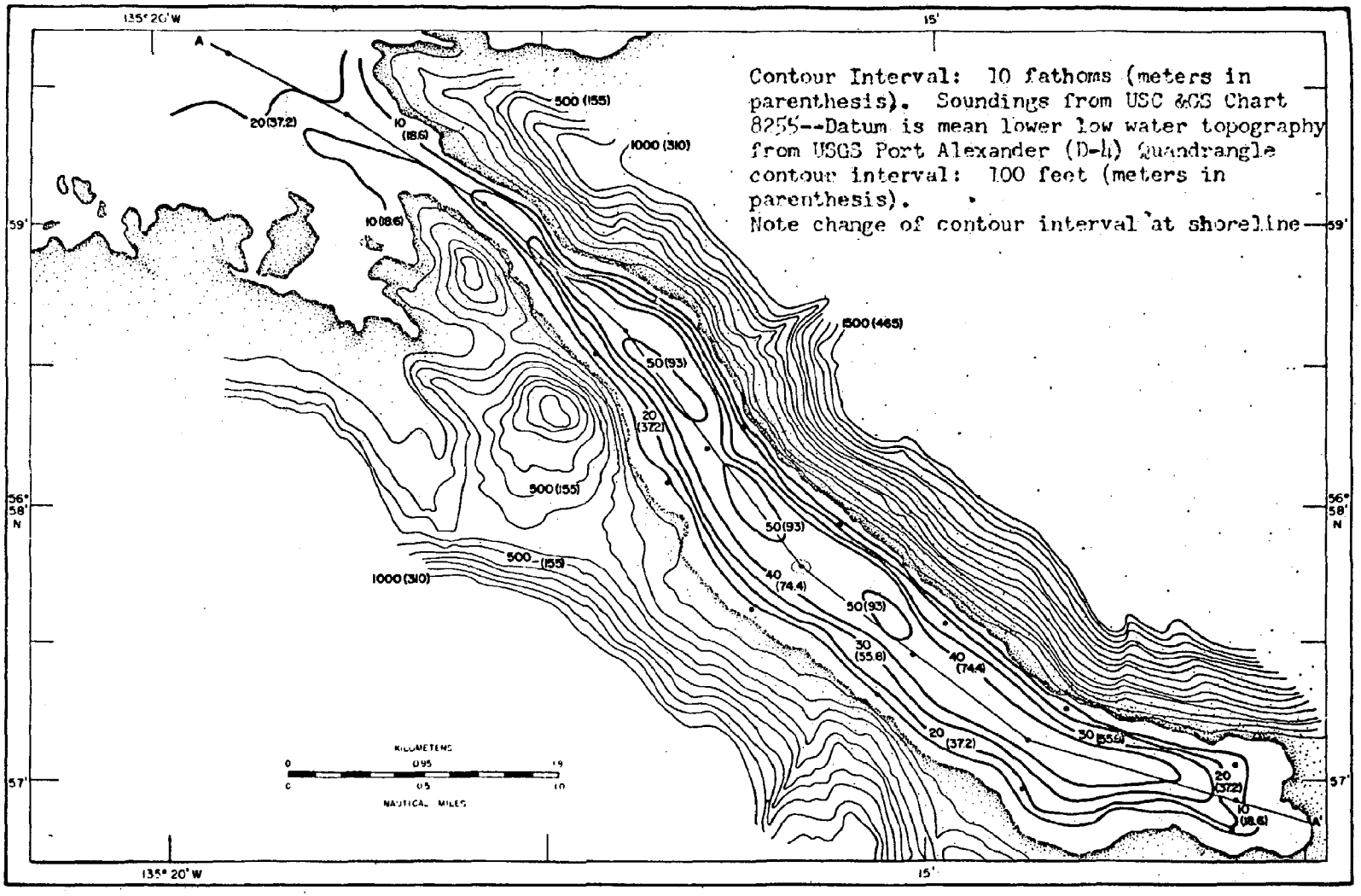


Fig. 1. Bathymetry of Deep Inlet, Alaska. From Andersen (1962).

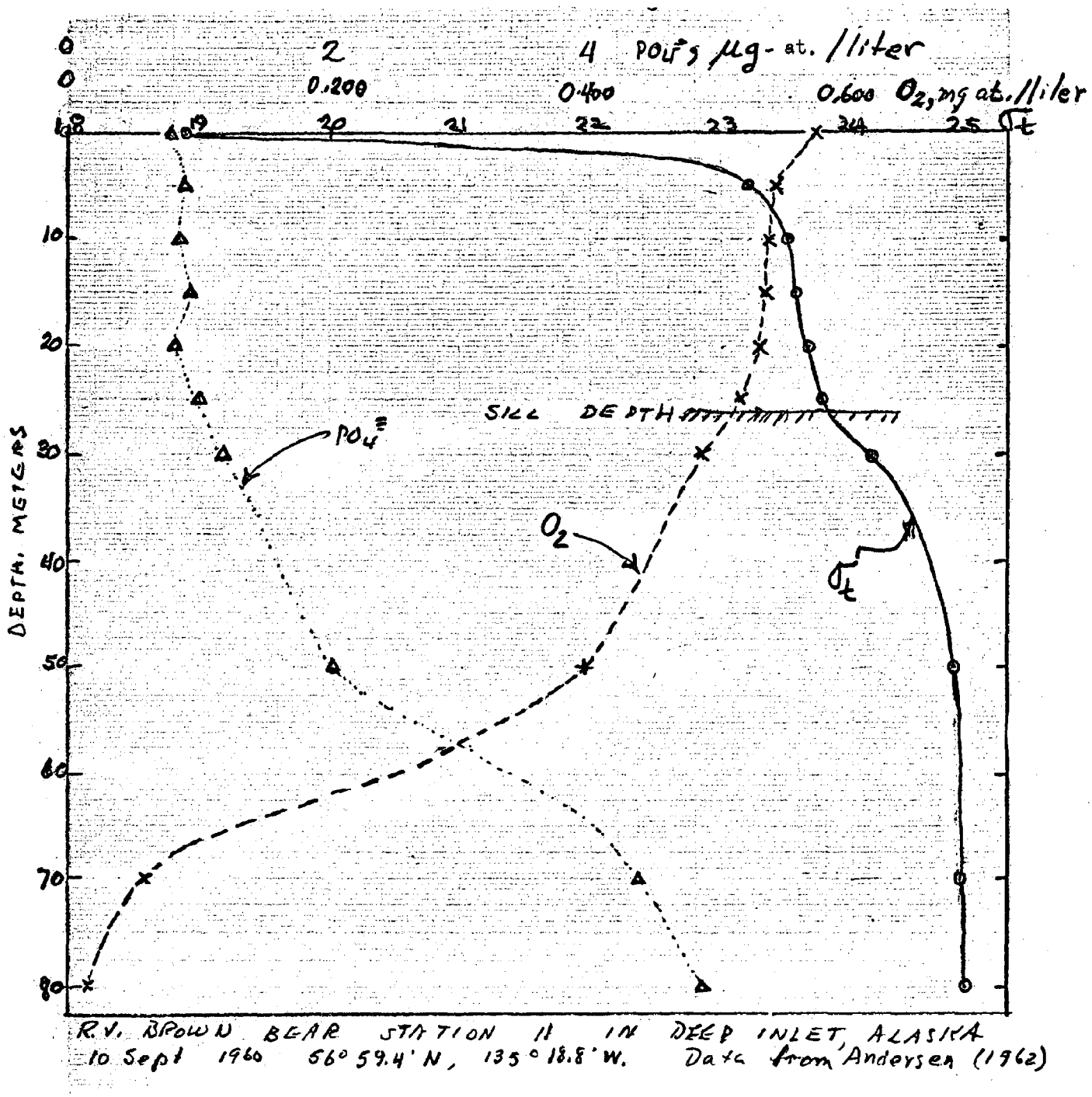


Fig. 2. Profiles of density (expressed in sigma-t units), dissolved oxygen, and inorganic phosphate in Deep Inlet, Alaska, 10 September 1960. A weak pycnocline exists below sill depth, a condition that favors stagnation. The loss of dissolved oxygen and the near-bottom accumulation of phosphates indicate stagnation, although there is still some dissolved oxygen throughout the water column. Data from Andersen (1962).

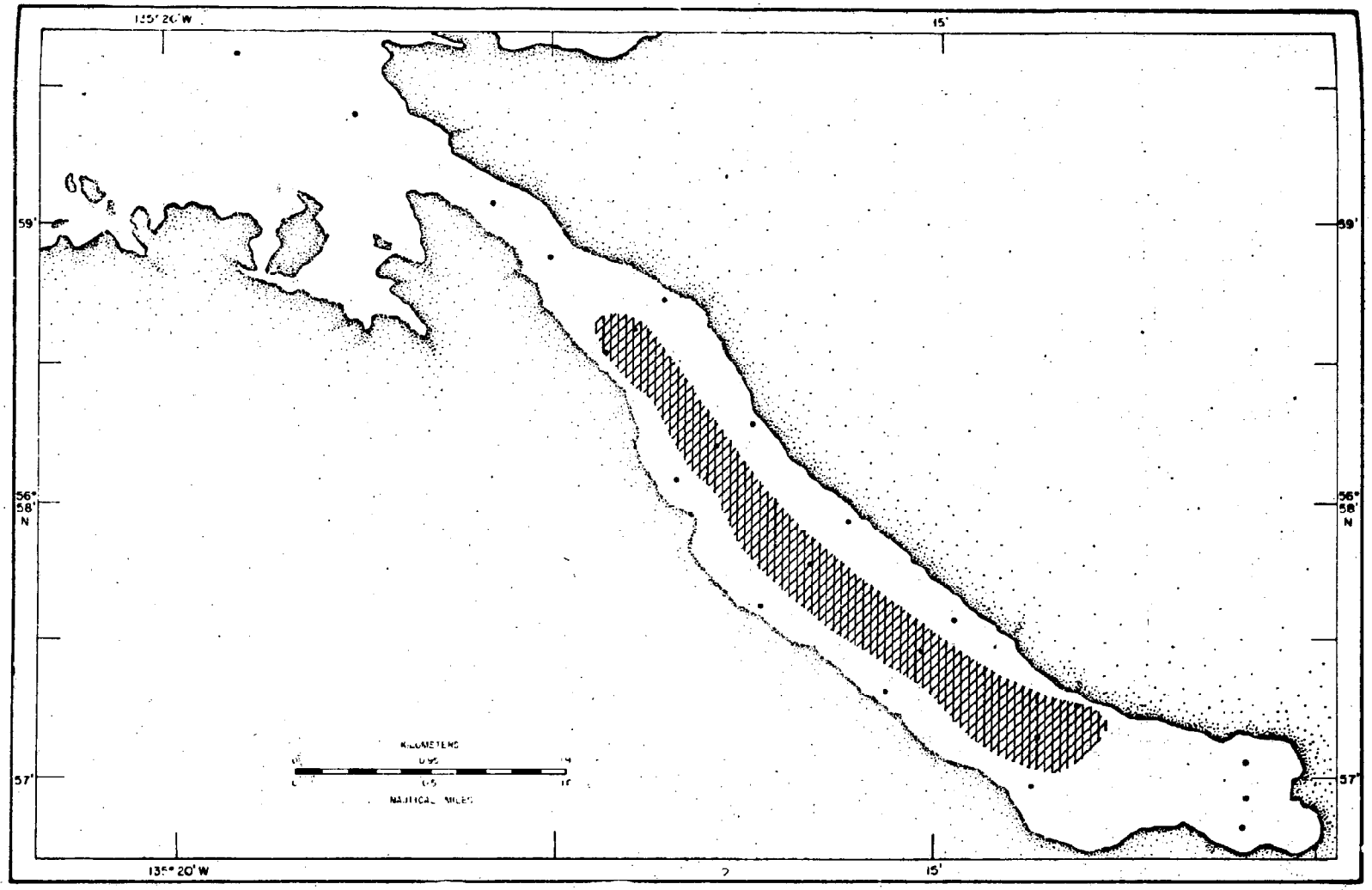


Fig. 3. Horizontal distribution of sulfides in the sediments of Deep Inlet, Alaska. From Andersen (1962).

better), and so the water coming in over the sill would be only weakly effective in flushing the system. The sediments in all the central part of the inlet contained hydrogen sulfide (Fig. 3), although no water samples were completely devoid of dissolved oxygen. It is evident that this is a weakly stratified fjord and might be subject to deterioration if the balance of nature were disturbed. Only one set of observations from the inlet is available (September, 1960), so nothing certain can be said of the seasonal cycle, but the system probably flushes in the winter, much as Saanich Inlet does.

Other Alaskan inlets: There are myriads of inlets and threshold fjords in Alaska, of which many remain oceanographically unexplored. Pickard (1967) reported on the oceanographic charcteristics of 15 inlets in southeast Alaska. Many of them have sills or subsystems with sills, and several showed a decrease in oxygen in the deeper water. However, no oxygen-free water was found and their flushing characteristics are generally unknown.

There are two rather simple natural fjords on Vancouver Island, British Columbia, which differ markedly in that one, Saanich Inlet (Figs. 4, 5, 6, 7) appears to flush annually, while the other, Lake Nitinat (Figs. 8, 9,10, 11,12)never flushes completely and always contains sulfides in its deeper water.

Puget Sound (Figs. 13, 14, 15, 16) is a complete fjord system of sub-basins separated by sills. Some of the subsystems circulate freely and are well ventilated, but some parts of the system, for example Dabob Bay and Lynch Cove on Hood Canal and Port Susan, tend to stratify and become oxygen deficient. Fig. 13 shows the major sills and basins. The sound is characterized generally by deep basins and vigorous circulation, so that only a few of the small subsystems tend to stagnate. Most of these flush during winter, but occasionally the winter flushing is incomplete.

Three subsystems of Puget Sound that tend to stagnate were described by Barnes and Collias (1958).

a. Dabob Bay: This is part of the Hood Canal subsystem of Puget Sound. The sill at the entrance to Hood Canal is 50 m deep, while the sill at the mouth of Dabob Bay is 130 m deep; the maximum depth in the bay is 190 m. Water was sampled at 180 m inside the sill eight times, from 22 February to 22 September, 1953. The temperature and salinity characteristics of the water remained constant, but the dissolved oxygen gradually decreased from 4.03 to 1.08 ml/liter at a practically uniform rate of 0.012 ml/liter/day. By 16 November, at least a significant fraction of this water was replaced, but stagnation recurred, beginning in March the next year. Between 25 March and 17 June, 1954, oxygen disappeared at the rate of 0.010 ml/liter/day. By 30 September 1954, the oxygen content had dropped to 0.24 ml/liter.

b. Port Susan: This system has a sill depth of 100 m and a maximum depth of 125 m. The oxygen content at 120 m decreased at a rate of 0.017 ml/liter/day between 23 September 1953 and 12 January 1954, dropping from 3.36 ml/liter to 1.47 ml/liter.

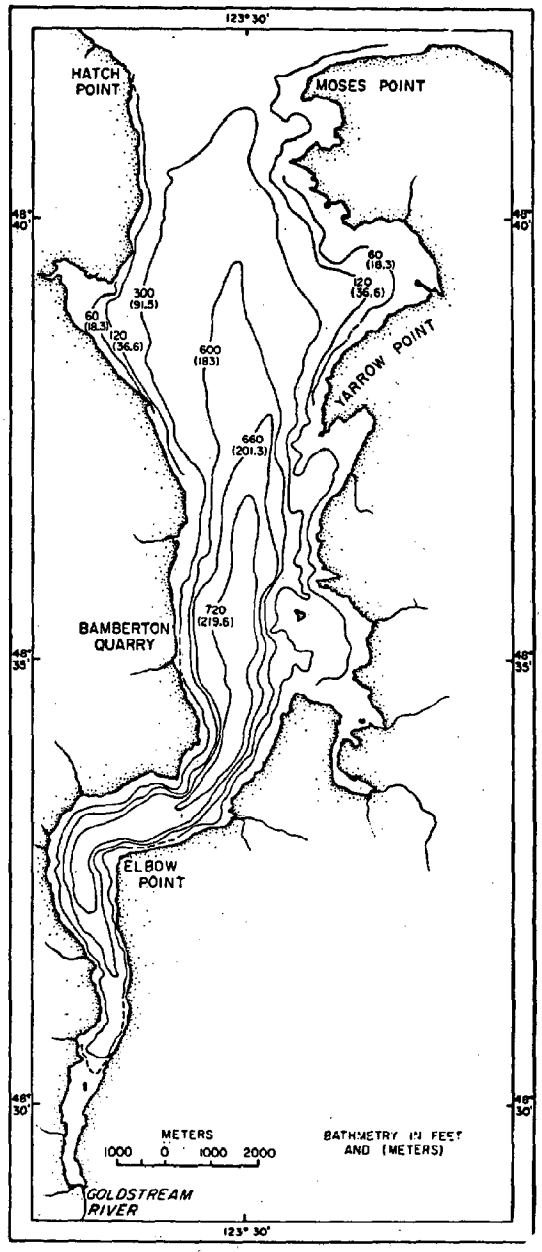
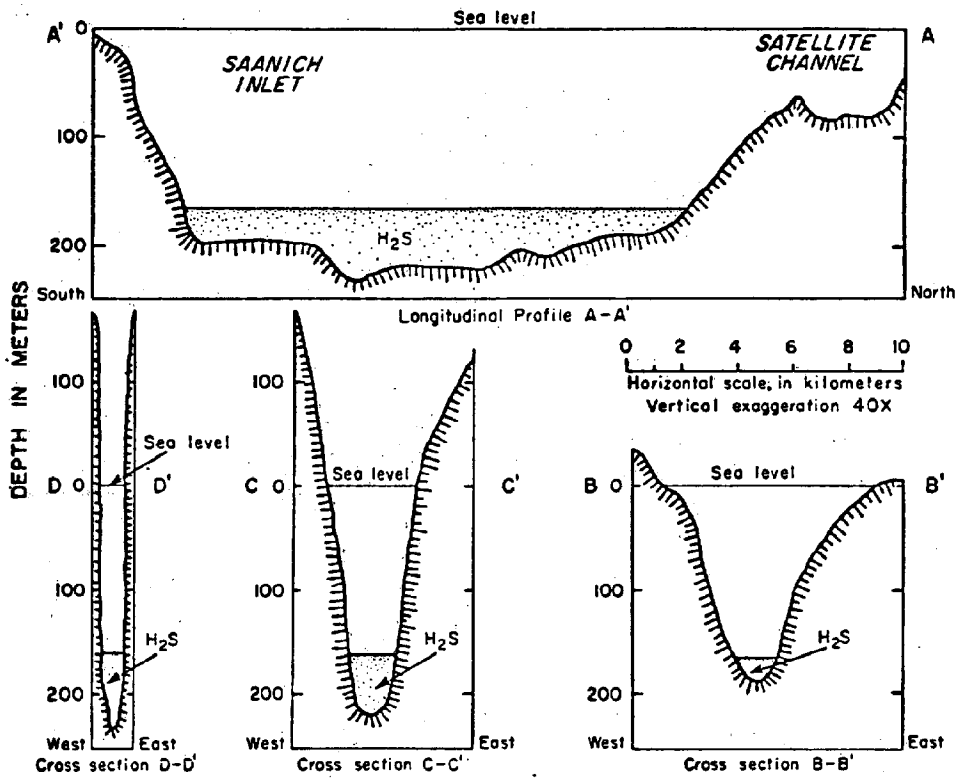
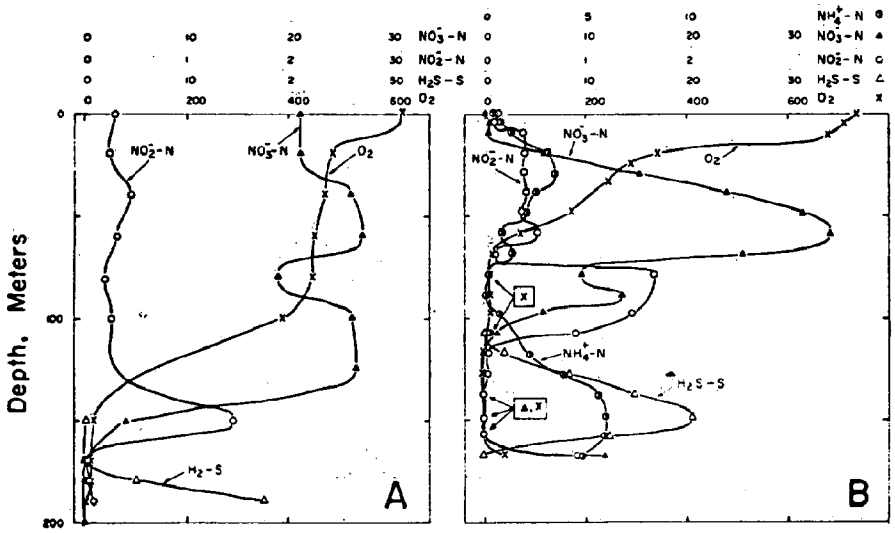


Fig. 4. Bathymetry of Saanich Inlet, Vancouver Island, British Columbia. The sill between Hatch Point and Moses Point is about 90 meters deep. From Gucluer (1962).



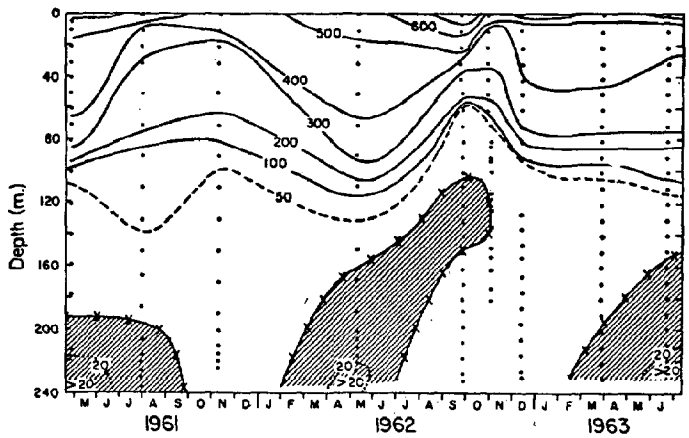
Longitudinal and cross-sectional profiles of Saanich Inlet, showing the approximate limits of the hydrogen sulfide-bearing water observed in November 1961 (F. A. Richards, personal communication).

Fig. 5. Longitudinal and cross sectional profiles of Saanich Inlet. From Gucluer and Gross (1964).



Vertical distribution of chemical properties in Saanich Inlet.
A—48°37.4′ N lat, 123°30.0′ W long, May 4, 1962.
B—48°31.8′ N lat, 123°32.0′ W long, September 12, 1962. Note that in *A* the anoxic zone is on the bottom while in *B* it is displaced upward from the bottom, at 198 m. The high concentrations of NO_2^--N lying above and below the sulfide zones apparently represent an intermediate phase of denitrification.

Fig. 6. Vertical distribution of chemical properties in Saanich Inlet. From Richards (1965b).



Regime of dissolved oxygen and H_2S in Saanich Inlet, Vancouver Island, British Columbia, April, 1961 to June, 1963. Oxygen and sulphide isopleths are in μg.-at./l. The shaded areas represent waters in which H_2S was present. The H_2S was observed only at mid-depths near the end of September, 1962, and probably represented water which had been displaced upward by an influx of water denser than that at the bottom at the time of the preceding observations. ——, - - - -, oxygen isopleths; —×—×—, boundary between oxygen and H_2S zones; . . . ., H_2S isopleths.

Fig. 7. Regime of dissolved oxygen and H_2S in Saanich Inlet. From Richards (1965a).

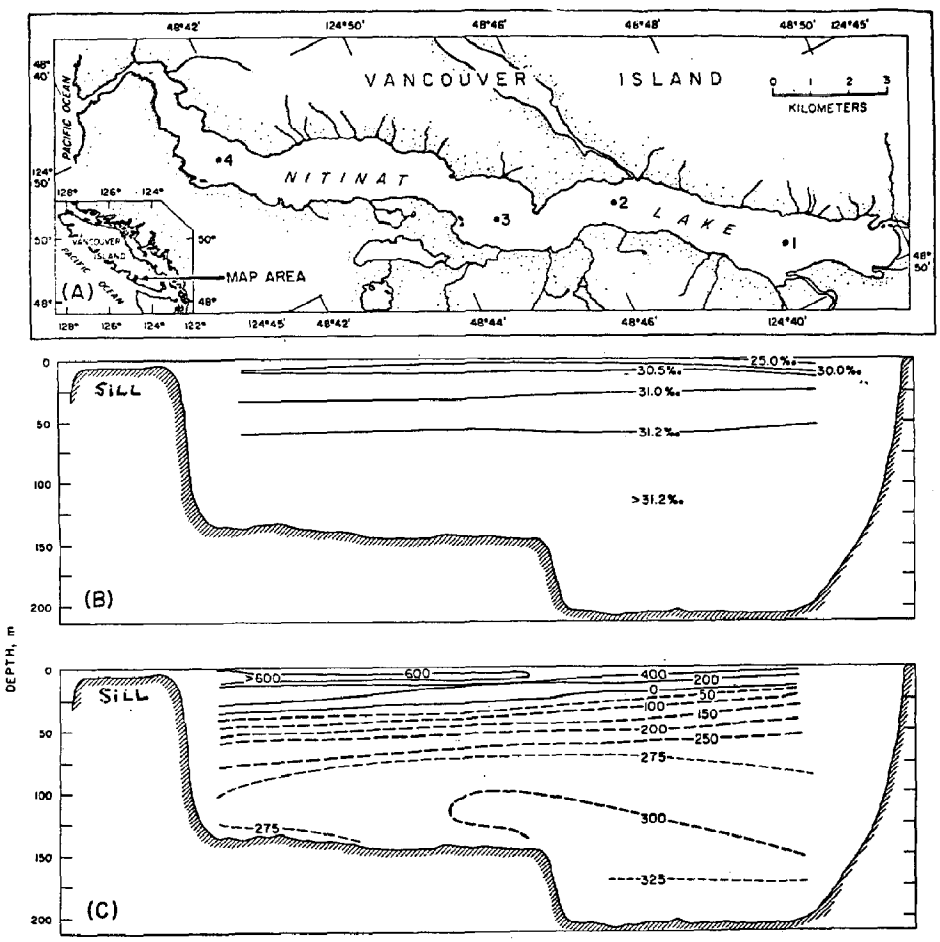
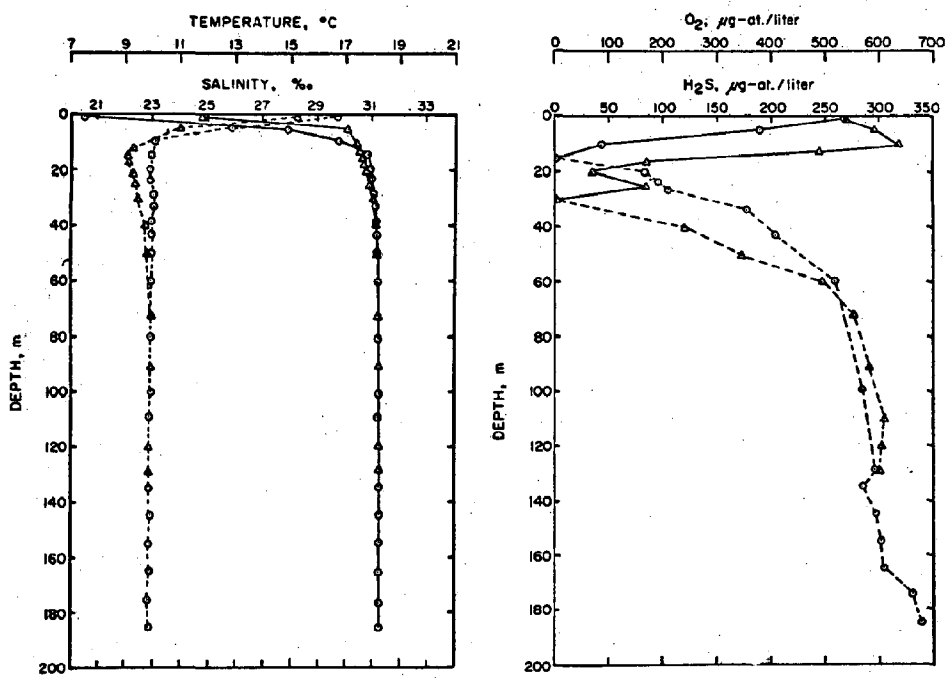


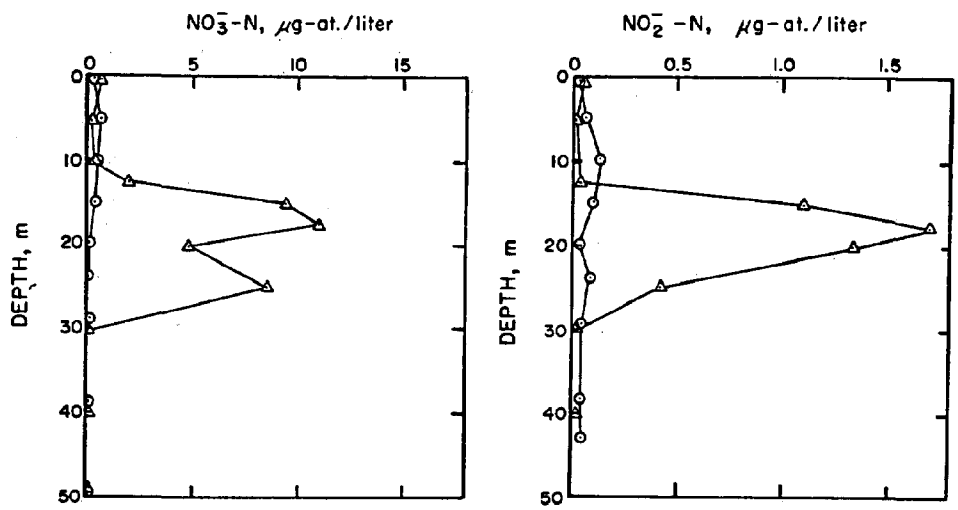
Fig. 8. Map of Lake Nitinat and vertical distributions of salinity, dissolved oxygen, and hydrogen sulfide. From Richards, Cline, Broenkow, and Atkinson (1965).



Vertical distributions of temperature---and salinity—at Stations 1 (○) and 3 (△) June 1965.

Vertical distributions of dissolved oxygen—and hydrogen sulfide---at Stations 1 (○) and 3 (△) June 1965.

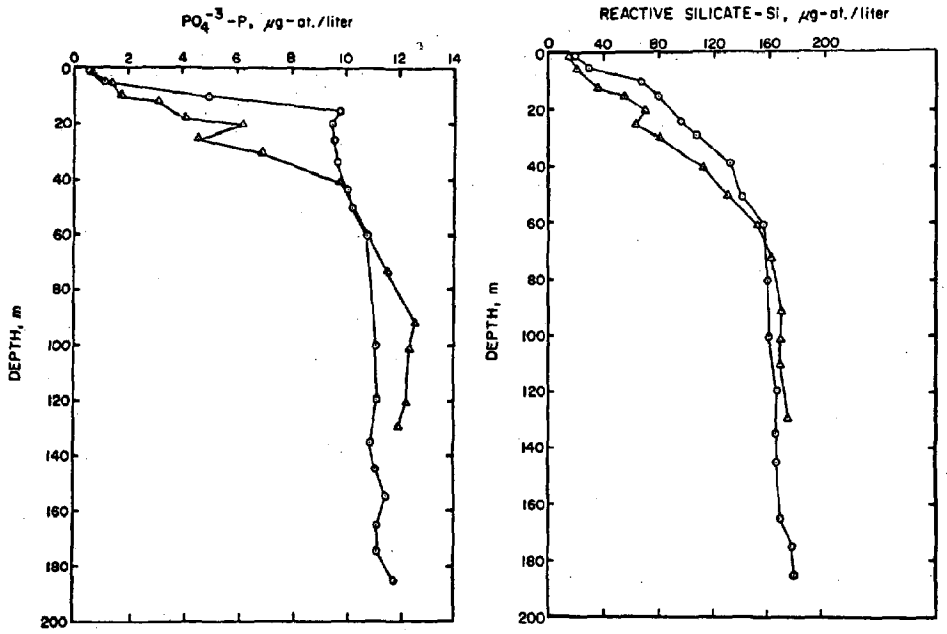
Fig. 9. Vertical distributions of temperature, salinity, oxygen, and H_2S in Lake Nitinat. From Richards et al. (1965).



Vertical distribution of inorganic nitrate-nitrogen at Stations 1 (○) and 3 (△) June 1965.

Vertical distribution of inorganic nitrite-nitrogen at Stations 1 (○) and 3 (△) June 1965.

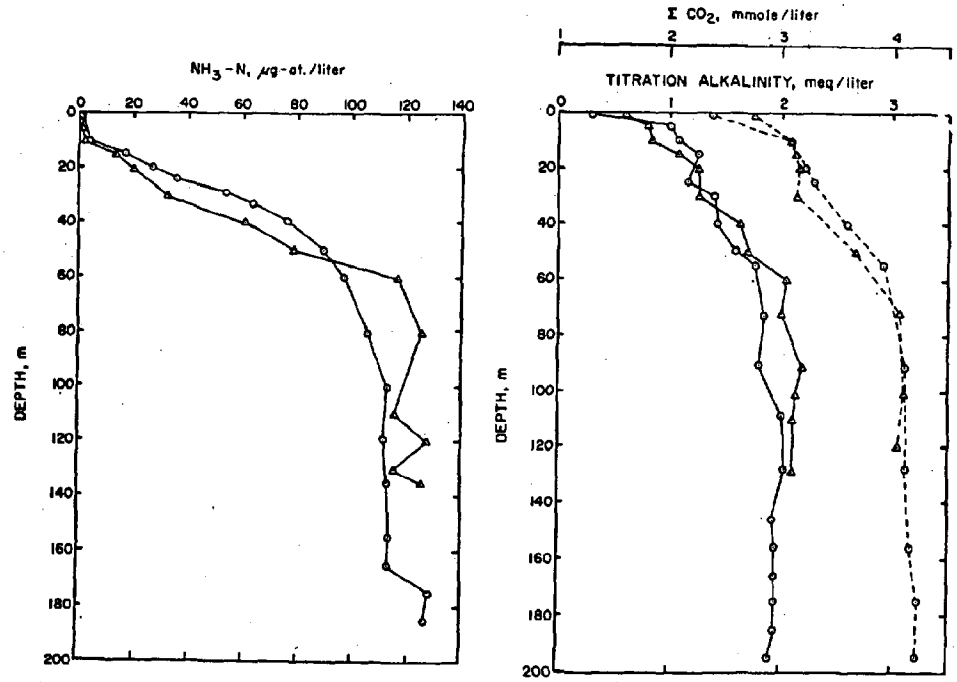
Fig. 10. Vertical distributions of nitrate and nitrite in Lake Nitinat. From Richards et al. (1965).



Vertical distribution of inorganic phosphate-phosphorus at Stations 1 (○) and 3 (△) June 1965.

Vertical distribution of reactive silicate-silicon at Stations 1 (○) and 3 (△) June 1965.

Fig. 11. Vertical distributions of inorganic phosphates and reactive silicates in Lake Nitinat. From Richards *et al*. (1965).



Vertical distribution of ammonia-nitrogen at Stations 1 (○) and 3 (△) June 1965.

Vertical distributions of total carbon dioxide—and titration alkalinity---at Stations 2 (○) and 3 (△) June 1965.

Fig. 12. Vertical distributions of ammonia, carbon dioxide, and titration alkalinity in Lake Nitinat. From Richards *et al*. (1965).

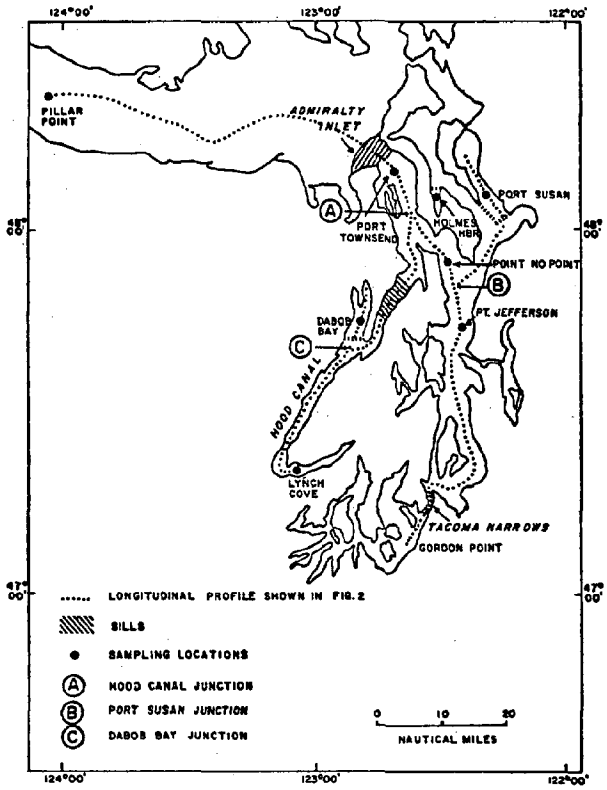


Fig. 13. Plan view of Puget Sound, Washington, showing sills and locating the longitudinal sections shown in Fig. 4. From Barnes and Collias (1958).

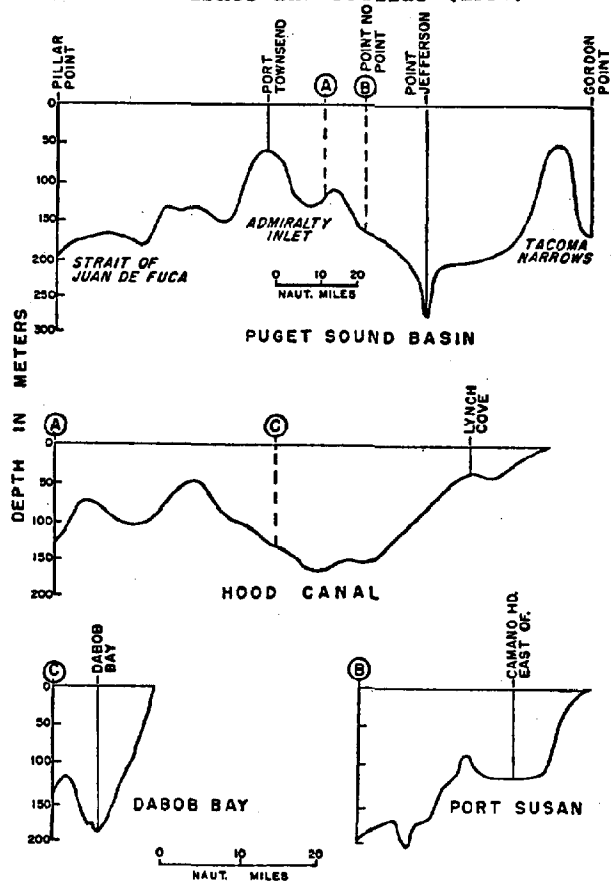


Fig. 14. Longitudinal section of Puget Sound, Washington, and of certain subsystems. From Barnes and Collias (1958).

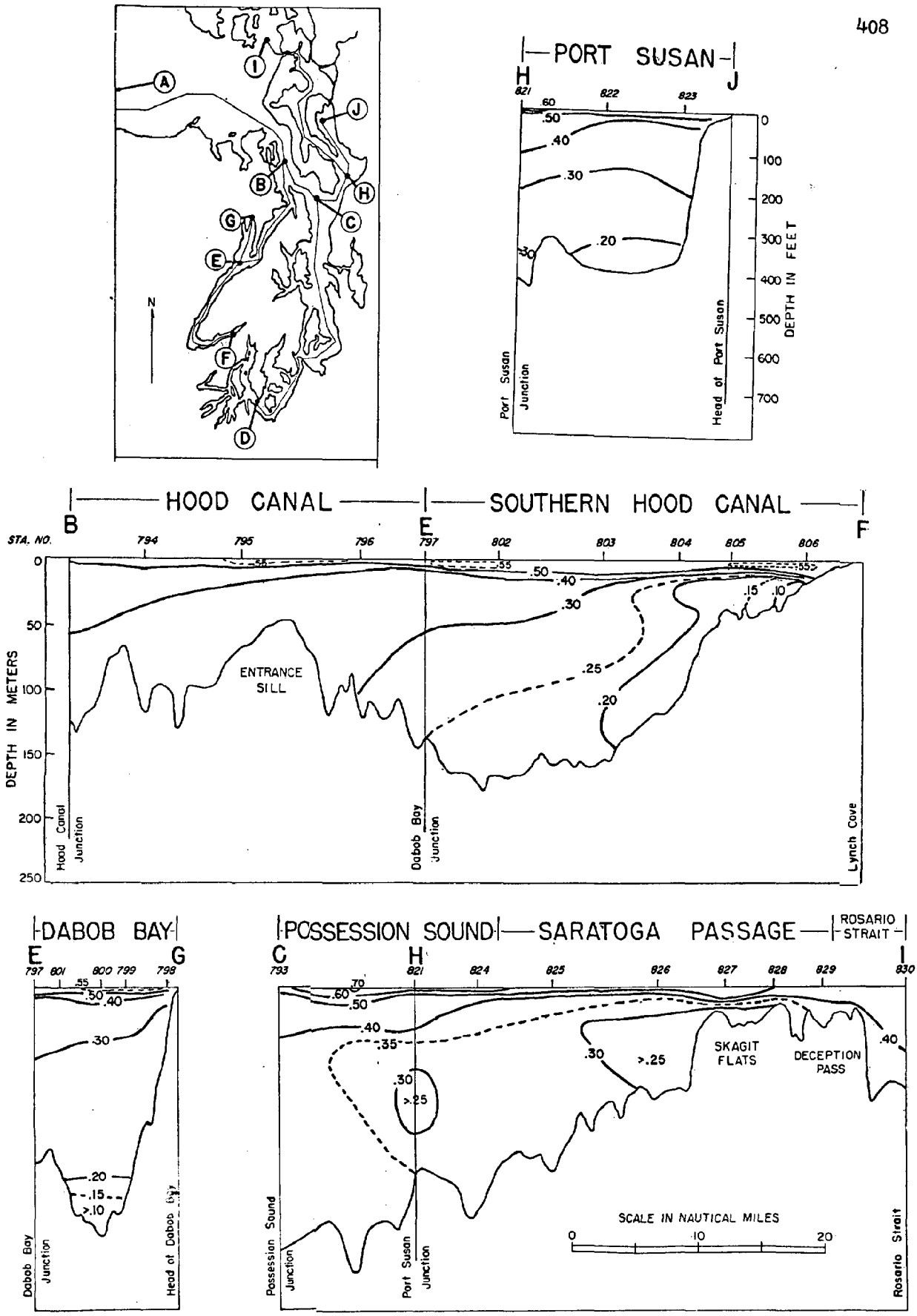


Fig. 15. Oxygen distributions in Puget Sound in summer (Univ. of Wash., Dept. of Oceanography, 1954).

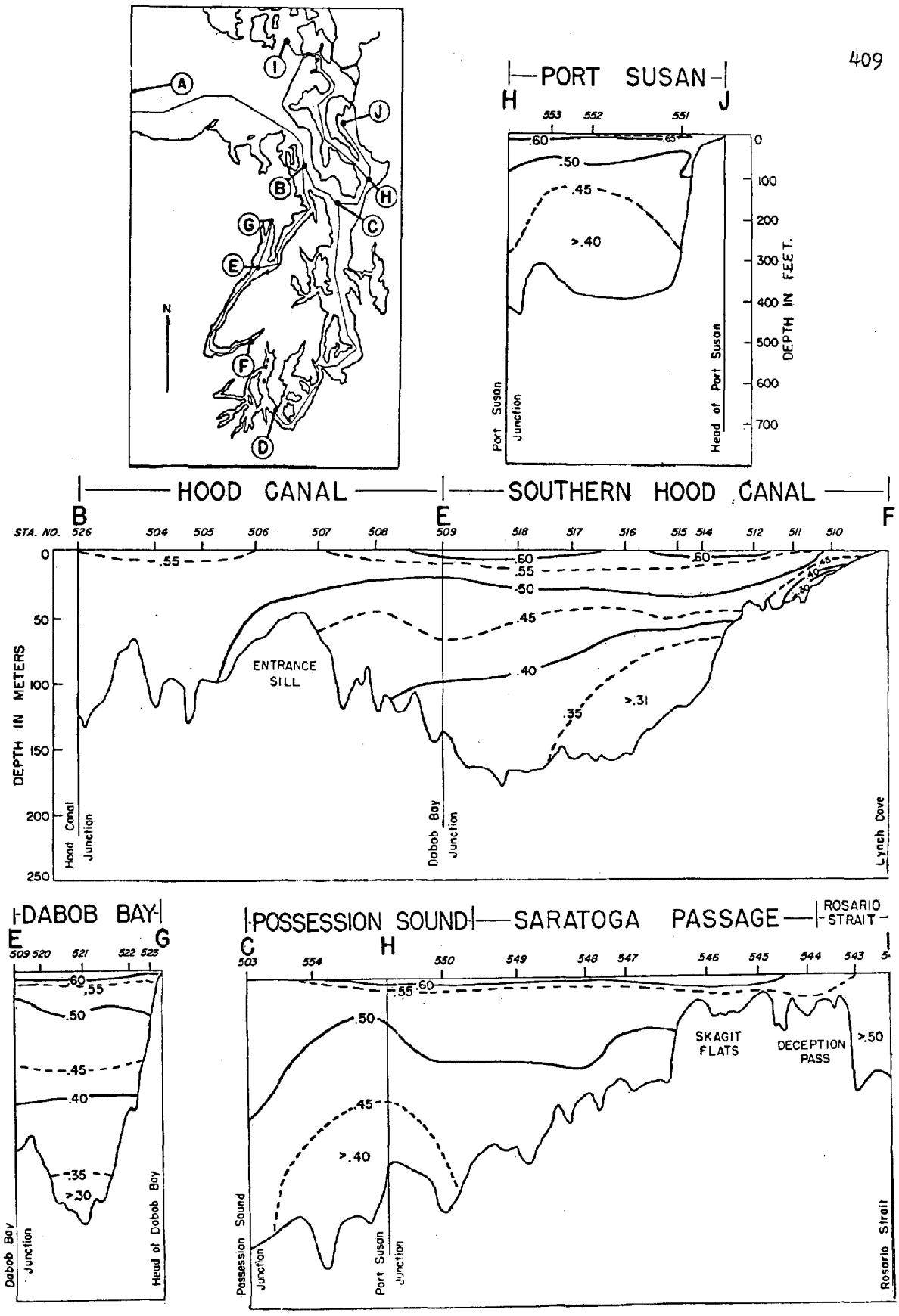


Fig. 16. Oxygen distributions in Puget Sound in winter (Univ. of Washington, Dept. of Oceanography, 1954).

c. Lynch Cove: This is a small, shallow (maximum depth 50 m) system separated from southern Hood Canal by a 35 m deep sill. In addition to the bar to circulation afforded by the sill, flushing is hindered by a horizontal constriction. Periods of decreasing oxygen contents were observed in the springs of 1958 and 1954 at rates of 0.020 and 0.018 ml/liter/day.

d. Other subsystems: There may be other stagnating systems in Puget Sound, for example, Dyes Inlet, but they have not been documented.

Fjords Receiving Large Quantities of Municipal Wastes

These systems are typified by Oslofjord, Norway. The two arms of the fjord inside Drøbak (Fig. 17), Vestfjorden and Bunnefjorden, receive or have received sewage with little or no treatment from the city of Oslo for years. The system is stratified, and parts of the inner fjord are constantly or intermittently stagnant, devoid of oxygen, and sulfide-containing (Ruud, 1968a). These conditions have resulted in a drastic reduction of the fisheries of the fjord and deterioration of the use of the fjord as a resort for bathing, boating, and sport fishing (Figs. 18, 19, 20).

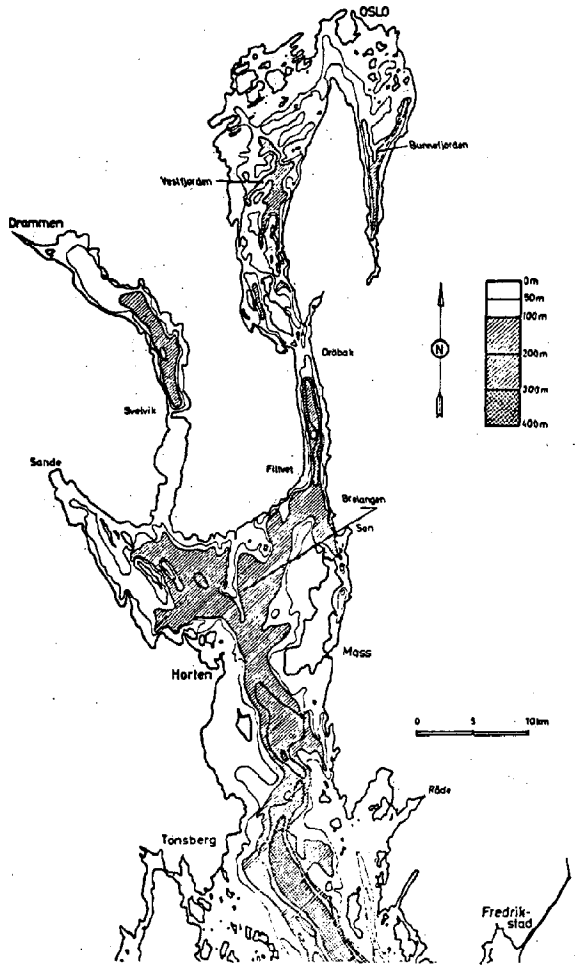
Another arm of Oslofjord is Dramsfjord (Fig. 21) which has a very limited circulation over the sill at Svelvik and receives some domestic and industrial sewage from the city of Drammen. It becomes anoxic and sulfide-bearing intermittently (Fig. 22), conditions that are probably aggravated by the influxes of wastes but which would probably arise, although to a lesser degree, from the entrapment and decomposition of naturally formed organic matter, much as is the case in Saanich Inlet.

Tropical Stratified Systems

Most of the systems that have been cited are in temperate climates, but some tropical environments are thermally stratified and become anoxic. An example is Kaoe Bay in Indonesia (Richards and Vaccaro, 1956), but little is known of the variations in its sulfide and oxygen contents. The Gulf of Cariaco (Fig. 23) on the north coast of Venezuela, has been better studied and is known to contain sulfides intermittently (Figs. 24, 25).

The Black Sea

The largest and possibly best known stratified, stagnant system is the Black Sea (Fig. 26). The sea receives more water by precipitation and river influx than it loses by evaporation, and receives saltwater from the Mediterranean Sea, via the Dardanelles, Sea of Marmora, and the Bosporus. It is therefore highly stratified and contains no oxygen from 125- to 150-m depths in the center and from around 250-m depths around its perimeter. Sulfide concentrations increase with depth to maximum concentrations of about 300 micromolar near the bottom (Fig. 27). These conditions affect the upper layers little if any, and the Black Sea supports normal fisheries and sports activities.



Bathymetric chart of the Oslofjord

Fig. 17. Bathymetric chart of Oslofjord. From Ruud (1968a).

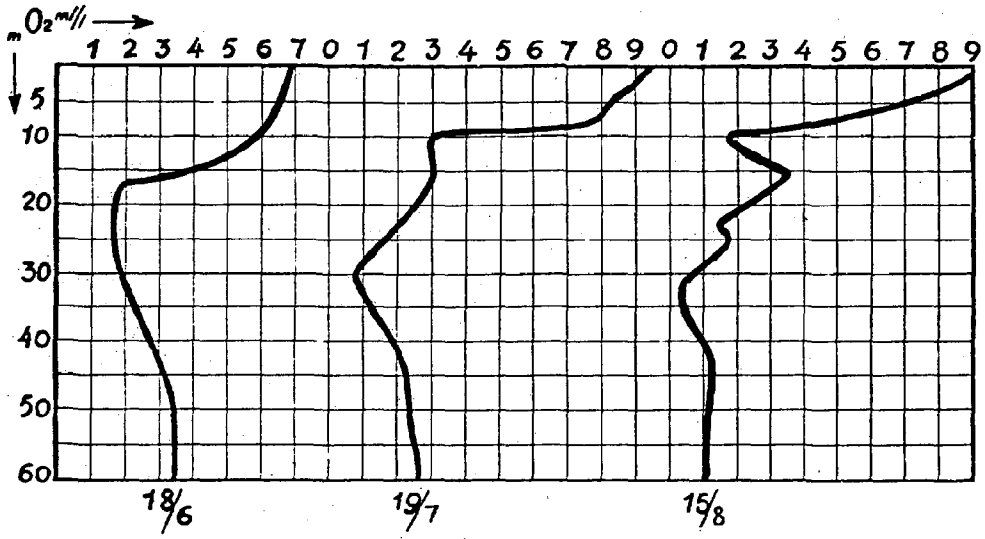
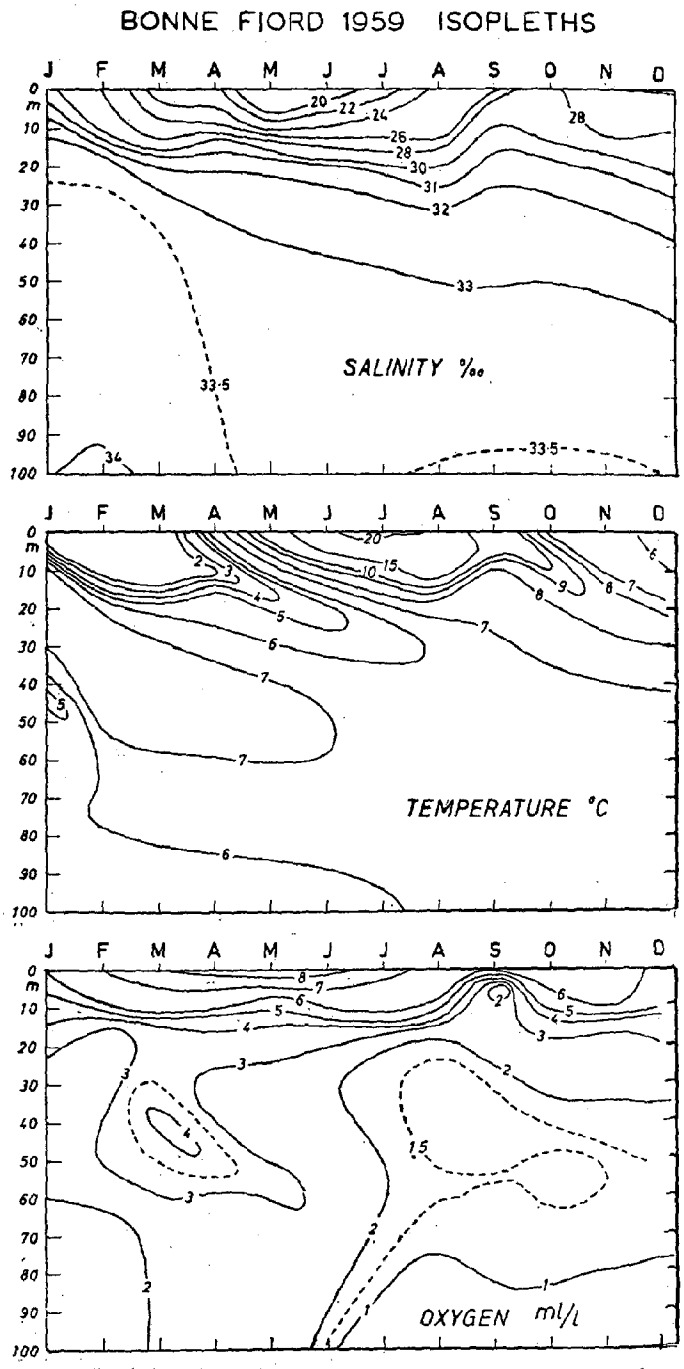


Fig. 18. Vertical distribution of dissolved oxygen in Oslofjord in summer. From Føyn (1960).



Isopleths of salinity, temperature and dissolved oxygen from "Berger", 1959.

Fig. 19. Seasonal variations in salinity, temperature, and dissolved oxygen at a station in the Bonnefjord section of Oslofjord. From Gade (1963).

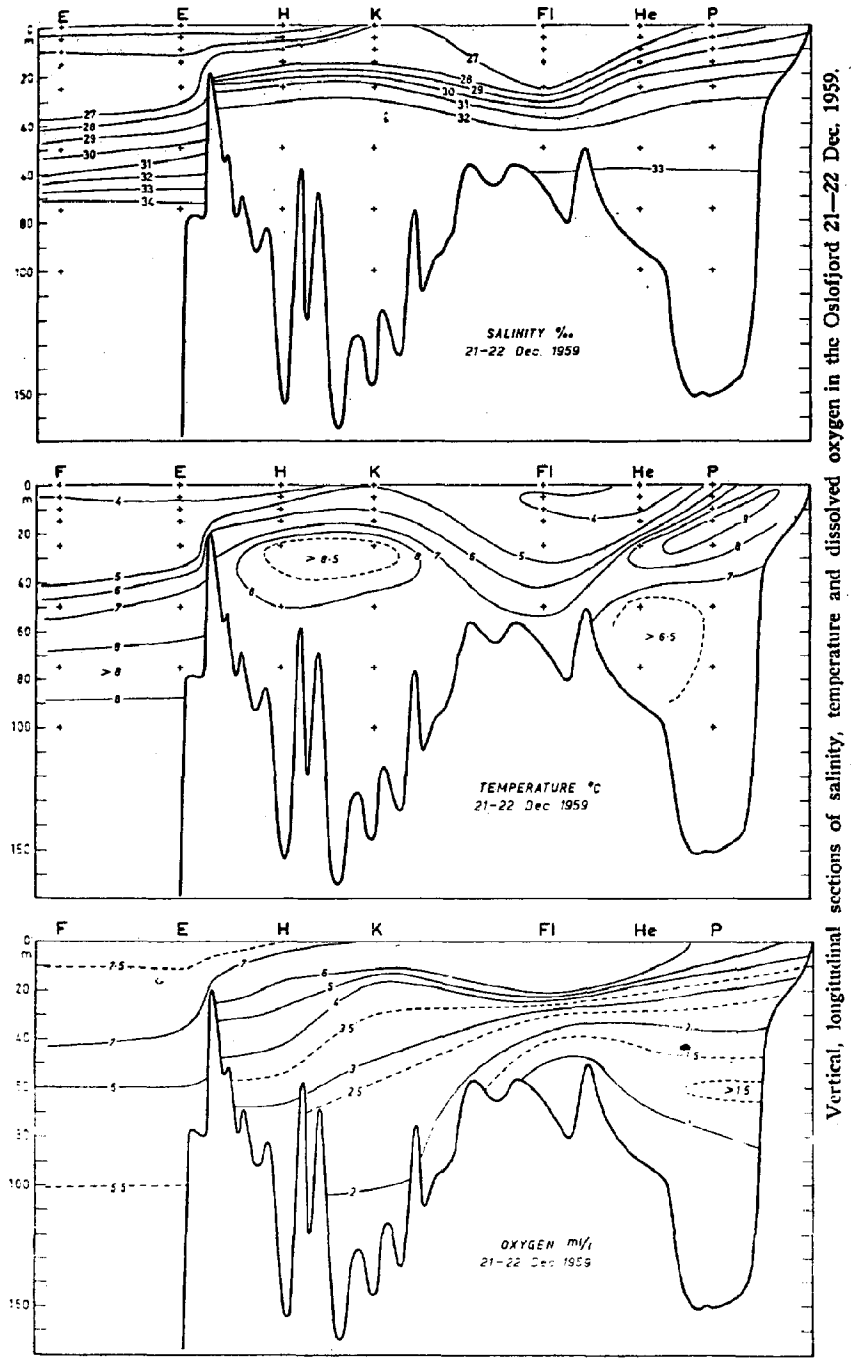
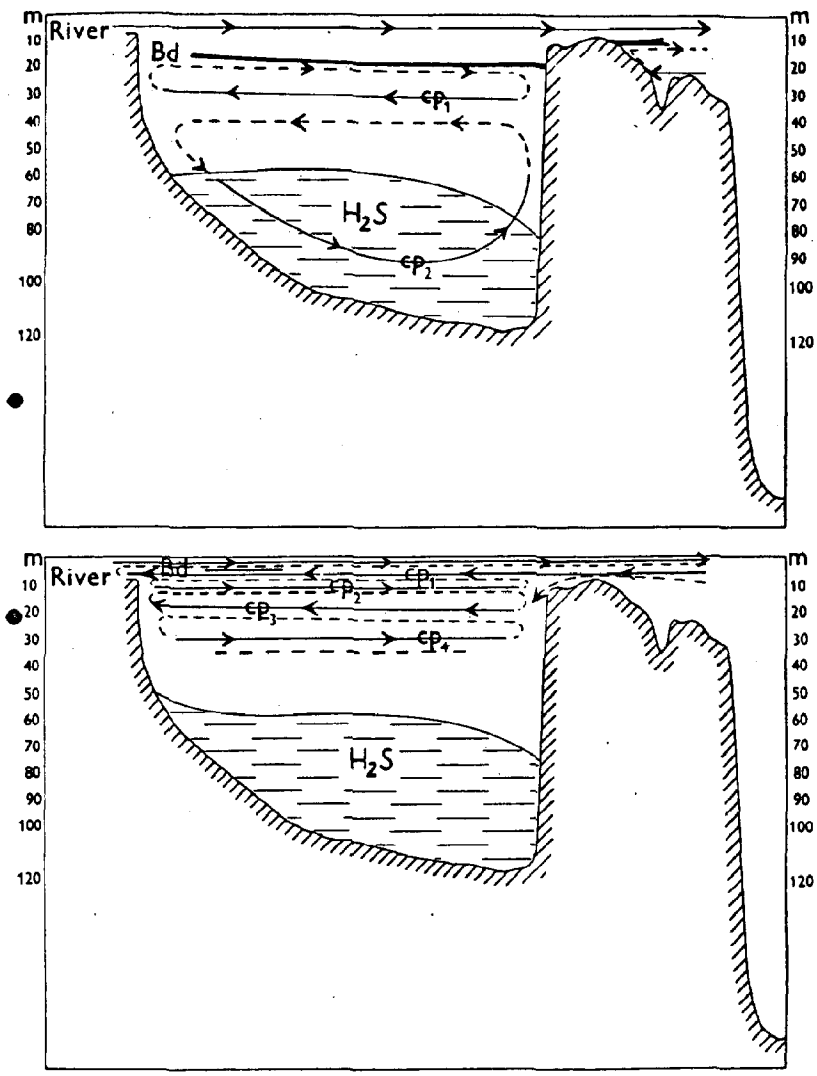
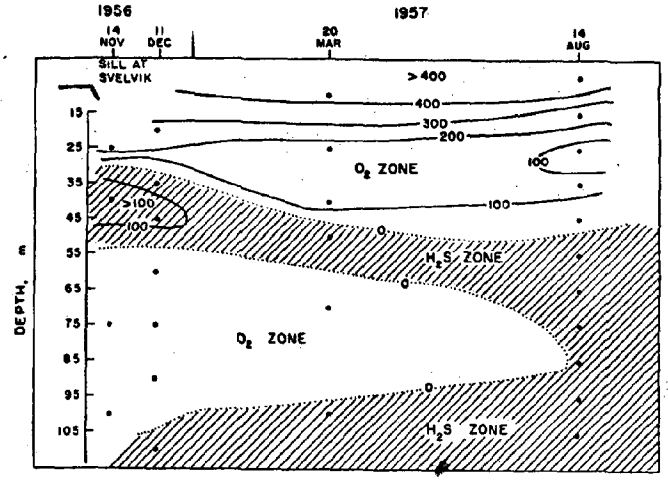


Fig. 20. Sectional distribution of salinity, temperature, and dissolved oxygen in Oslofjord in December 1959. From Gade (1963).



Water masses and the prevalent circulation patterns in the Dramsfjord in early *summer* (top figure, June) and *winter* (bottom figure, December). Bd = boundary between fresh (summer), or highly diluted (winter), and salt water. cp = compensation current. Mean velocities of surface flow 2.9 cm/sec. (June), and 1.3 cm/sec. (December), of the deeper currents very much less. (From Beyer, 1958.)

Fig. 21. Water masses and circulation in Dramsfjord, an arm of Oslofjord, in summer (above) and winter (below). From Braarud, Føyn, and Hasle (1953).



Vertical distribution of sulphides and dissolved oxygen at station bm in the Dramsfjord, 14 November 1956–14 August 1957. Concentrations are in microgramme atoms per litre.

Fig. 22. Regime of dissolved oxygen and sulfides in Dramsfjord, November 1959 - August 1957. From Richards and Benson (1961).

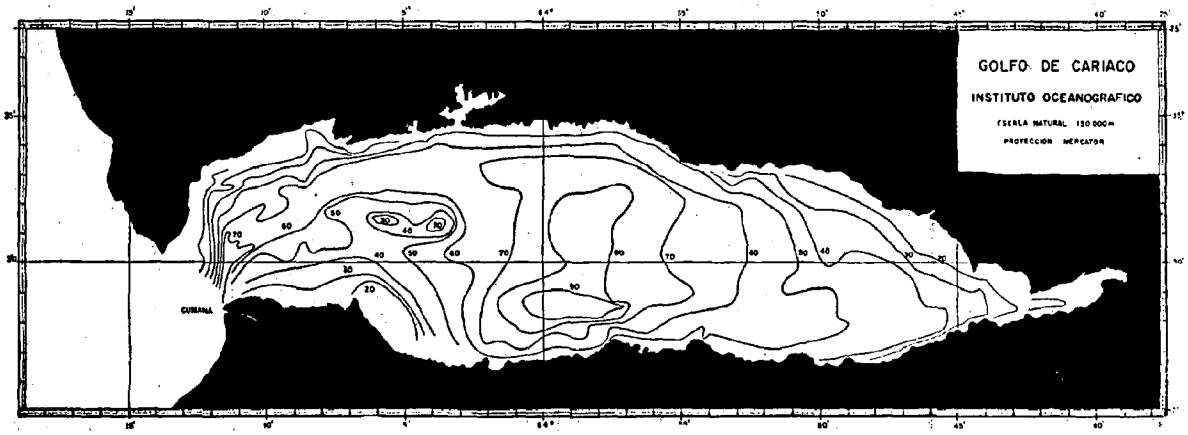
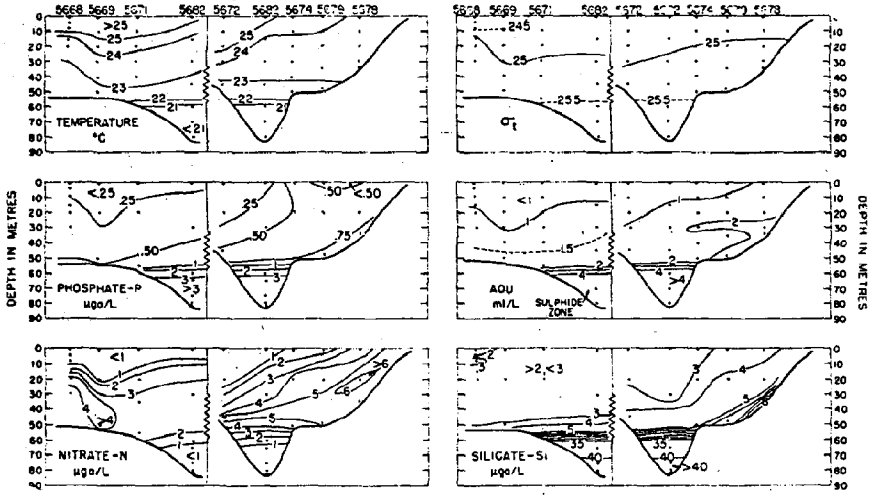


Fig. 23. Bathymetry of the Gulf of Cariaco, Venezuela. From Gade (1961).



Physical and chemical variables in a section along the length of the Gulf of Cariaco. Station locations are shown in FIG. 1.

Fig 24. Physical and chemical variables in Gulf of Cariaco in October 1958. From Richards (1960).

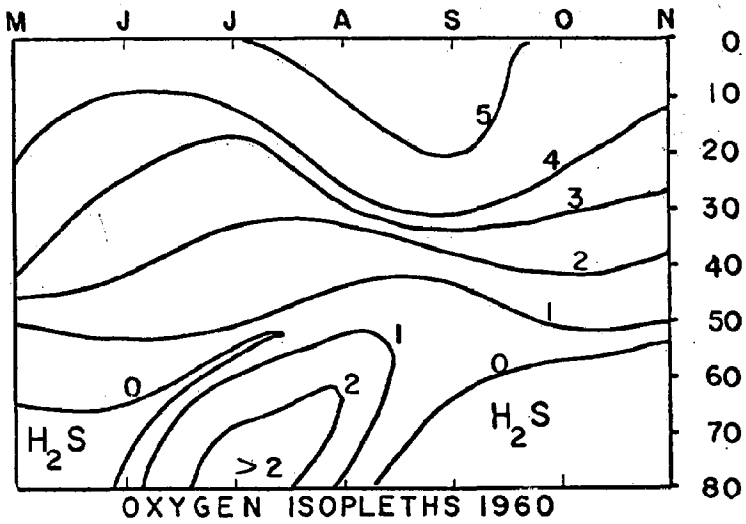
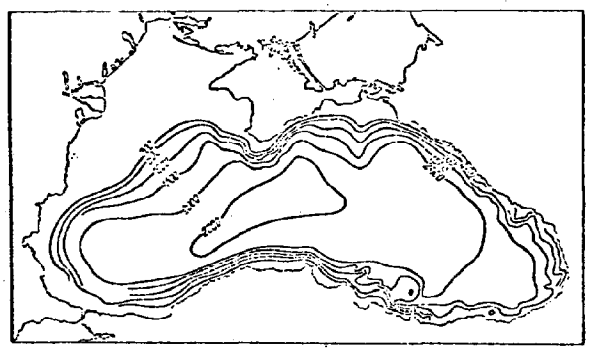
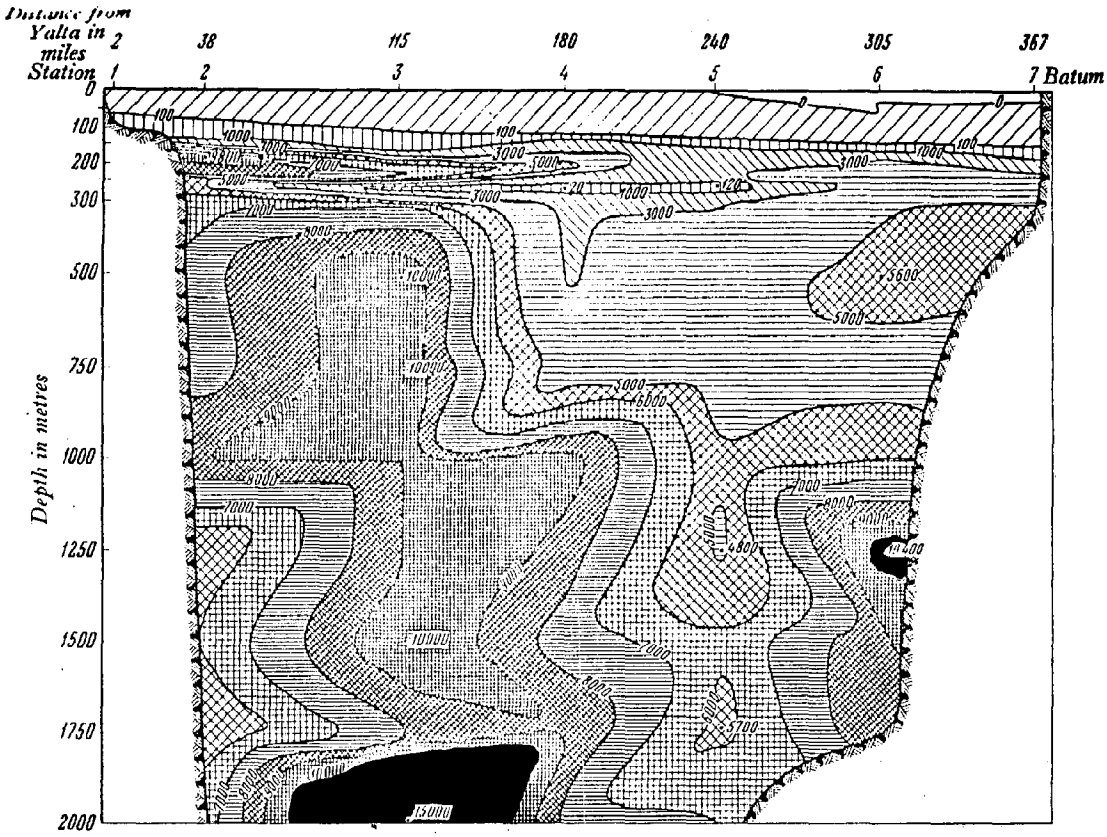


Fig. 25. Regime of dissolved oxygen and of hydrogen sulfide in the Gulf of Cariaco, 1960. From Gade (1961).



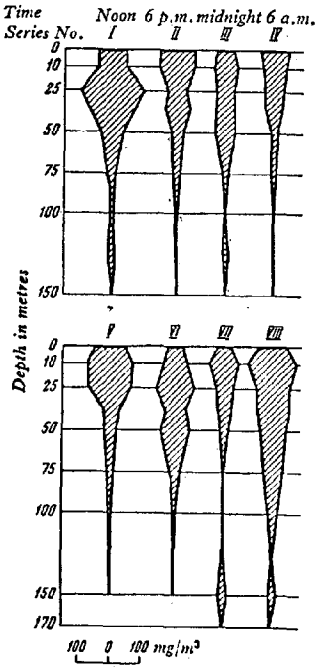
Bottom topography of Black Sea (Archangelsky and Strahov).

Fig. 26a. Bathymetry of the Black Sea.

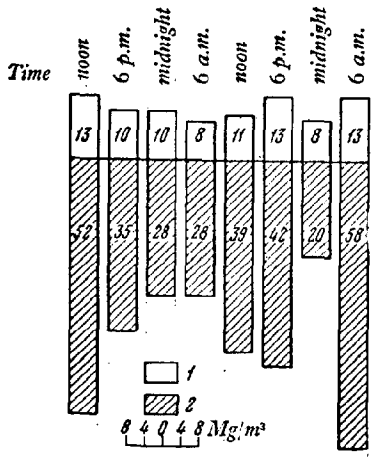


Distribution of the numbers of bacterial filaments in the section Yalta-Batum Feb. 1951 (from Thesis by M. N. Lebedeva).

Figures = number of microorganisms per ml of water.



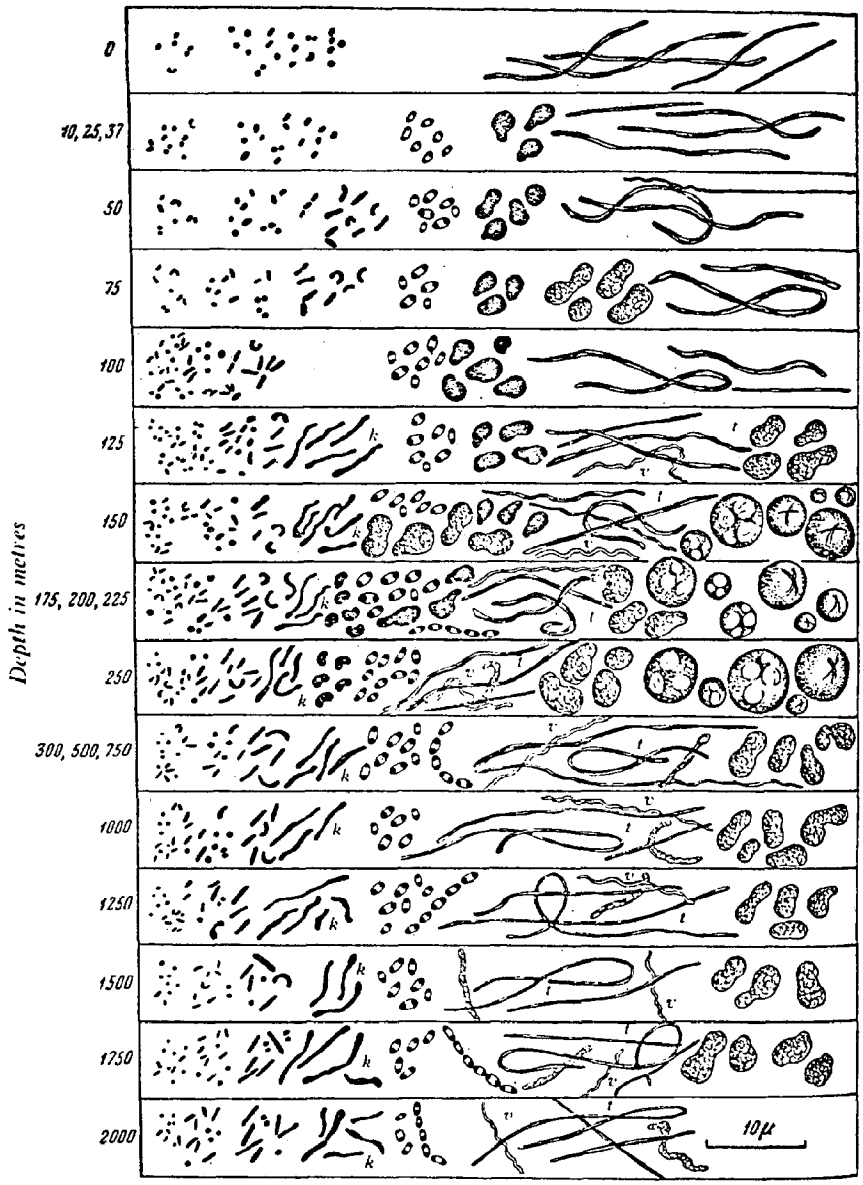
Diurnal fluctuations in the biomass of phytoplankton in the open part of the Black Sea (data from Morozova Vodyanitzkaya).



Diurnal changes in the biomass (mg/m³) of microorganisms and phytoplankton in the 0-150 metre water layer in the Black Sea (from Thesis by M. N. Lebedeva).

1. Microorganisms
2. Phytoplankton.

Fig. 26B Patterns of bacterial distribution in the Black Sea (Kriss,1963).



Morphological range of microorganisms at various depths of the Black Sea (on filters).

Fig. 26c. Bacteria in the Black Sea (Kriss, 1963).

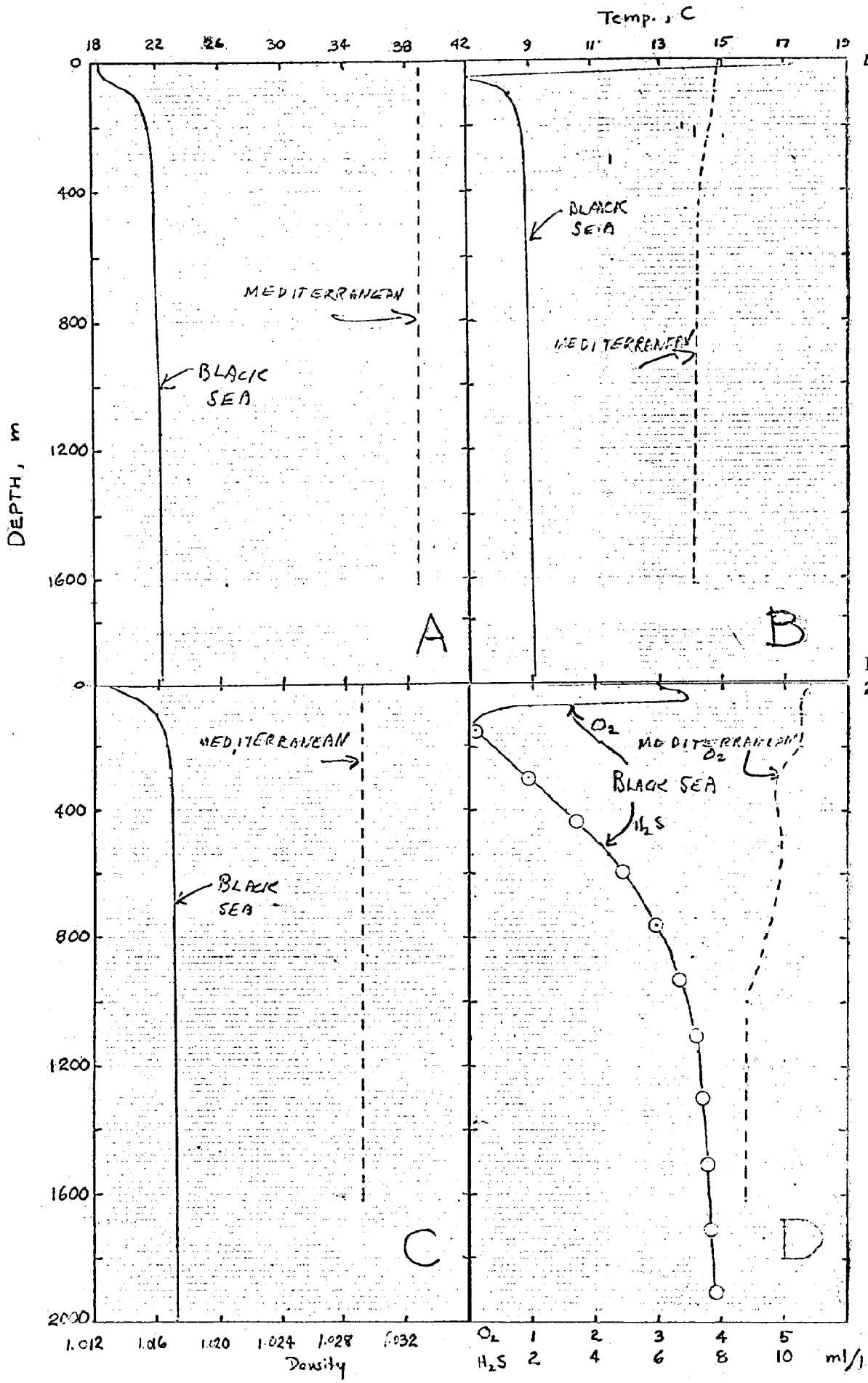

Temp., C
18
22
26
30
34
38
42
9
11
13
15
17
19
DEPTH, m
0
400
800
1200
1600
2000
MEDITERRANEAN
BLACK SEA
A
B
C
D
O2
H2S
1.012
1.016
1.020
1.024
1.028
1.032
Density
1
2
3
4
5
2
4
6
8
10
ml/l

Fig. 27A

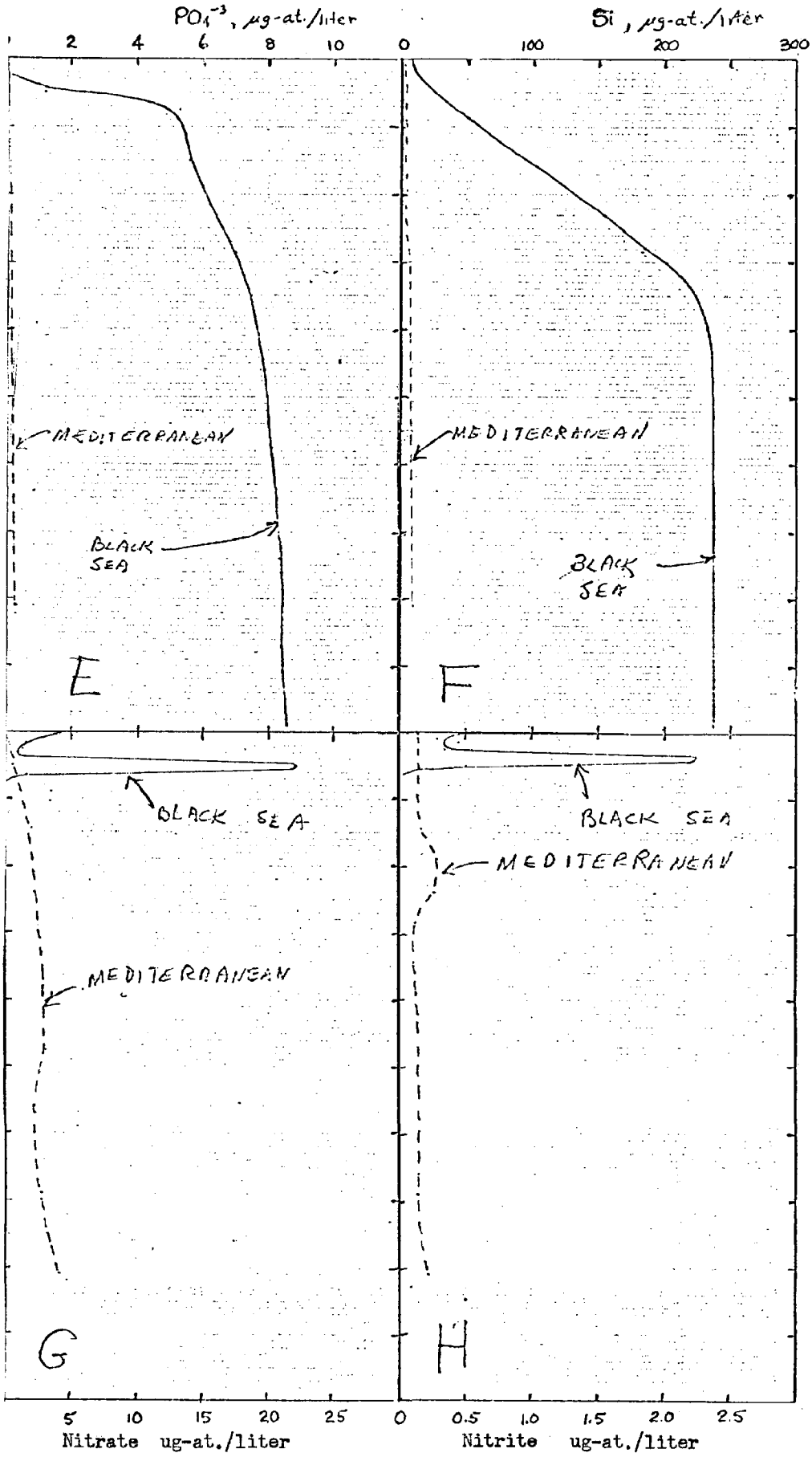
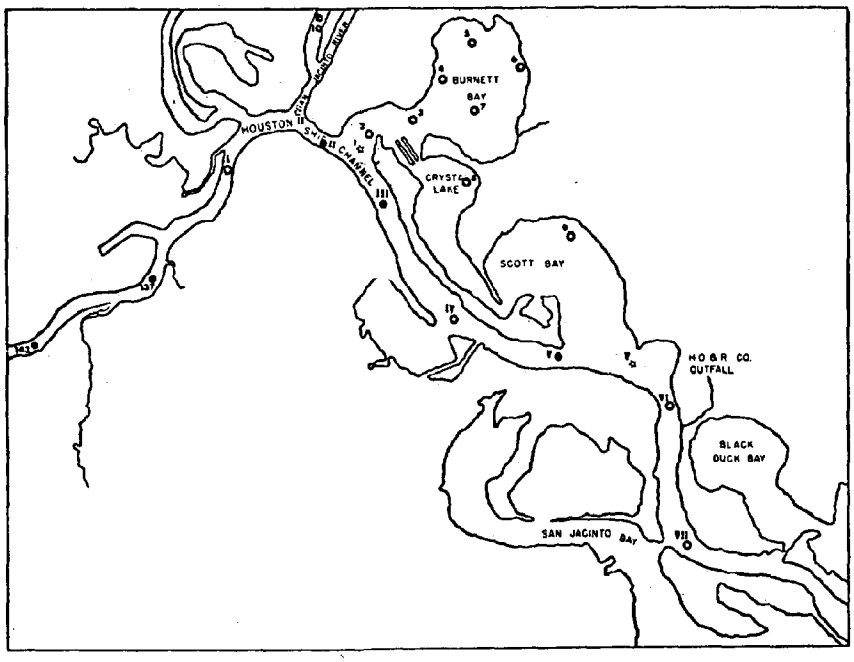

PO4-3, µg-at./liter
2
4
6
8
10
Si, µg-at./liter
0
100
200
300
MEDITERRANEAN
BLACK SEA
E
MEDITERRANEAN
BLACK SEA
F
BLACK SEA
MEDITERRANEAN
G
BLACK SEA
MEDITERRANEAN
H
5
10
15
20
25
Nitrate ug-at./liter
0
0.5
1.0
1.5
2.0
2.5
Nitrite ug-at./liter

Fig. 27B

Fig. 27
See previous page

Vertical distribution of chemical properties and of density in the Black Sea with comparative values from the Mediterranean Sea. The Black Sea values were observed at 41°58'N, 30°23'E on 29 September 1964. The Mediterranean values at 35°54'N, 25°15.5'E, on 30 March 1948. A. Salinity, in grams/kilogram; B. Centigrade temperature; C. Density of the water at the temperature given in B if brought to the sea surface; D. Dissolved oxygen and hydrogen sulfide concentrations, both in ml/liter; E. Phosphate-phosphorus concentrations, in microgram atoms/liter (millimoles/liter); F. Soluble silicate-silicon concentrations, in microgram atoms/liter; G. Nitrate-nitrogen concentrations, in microgram atoms/liter; H. Nitrite-nitrogen concentrations, in microgram atoms/liter.



Sampling Stations. Stars indicate stations sampled on September 1, 1957; black circles indicate stations after January 30, 1958.

Fig. 28. Houston Ship Channel. From Chambers and Sparks (1959).

Dredged Channels

The Houston Ship Channel (Fig. 28) is an example of a dredged channel that receives large quantities of industrial waste materials and heat. It is a salt-wedge estuary (Fig. 29) part of which becomes oxygen deficient (Fig. 30). Oxygen concentrations too low to sustain many species of fish have been observed in the system (Chambers and Sparks, 1959).

The Lake Washington Ship Canal is a special case of a dredged system that will be discussed later.

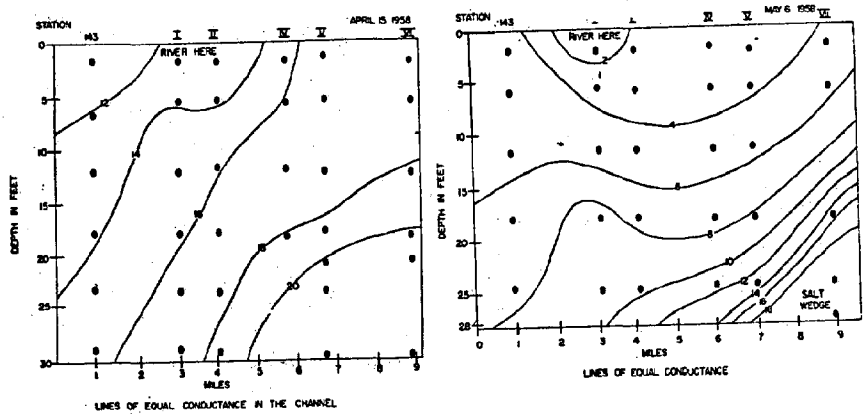
DISCUSSION

Stratification

Natural waters owe their density to their temperature, their salt content, and the pressure on them. The compressibility of water is slight, so the pressure effect on the density of waters at estuarine depths can be ignored for practical purposes. In stratified estuaries, the density of the water increases markedly from top to bottom, in distinction to the situation in unstratified estuaries. This stratification presents a marked hindrance to vertical mixing.

In all stably stratified waters, the water density increases continuously with depth, but the rate of increase may vary markedly (Fig. 31). It is characteristic of stratified estuaries that at some intermediate depth the rate at which the density increases with depth is more rapid than in the deeper or shallower water. This region is known as the pycnocline (from the Greek pycnos, thick, dense, and the Latin clinare, to bend, incline) (Fig. 31). In stratified estuaries in the temperate zone, the depth increase in density can generally be attributed primarily to increases in the salt content of the water, because river water entering the estuaries spreads out and floats on the deeper water, which is more saline because of influxes of seawater from the mouth of the system. This type of pycnocline is called a halocline. There may be considerable differences in the shape of the pycnocline, as is illustrated in Fig. 31. Thus, many stratified estuaries approach a three-layered system: 1) The upper layer is characterized by low-salinity water in which the density may increase only gradually with depth. In some systems, this upper layer may be mixed by the wind and show little if any increase in density with depth, and in some cases it may be virtually absent (see Fig. 31). 2) The intermediate layer, or pycnocline, through which the density increases rapidly with depth. This layer represents mixtures of the low-salinity overlayer and the deep saline layer. 3) The deep, saline layer in which the density increases relatively slowly with depth.

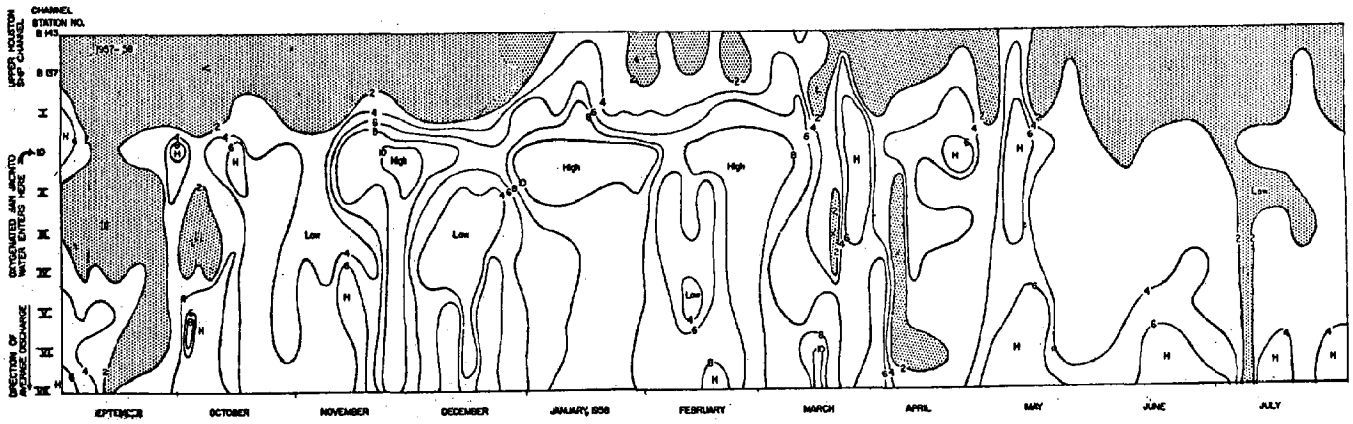
The stratified estuaries of the temperate zone usually owe their density structure to the non-uniform vertical distribution of salt in them



Lines of equal conductance ($\frac{\text{micromhos}}{\text{cm}} \times 10^3$) in the channel. April 15, 1958.

FIG. 10. Lines of equal conductance in the channel. May 6, 1958.

Fig. 29. Lines of equal conductance in Houston Ship Channel, 15 April 1958 (left) and 6 May 1958 (right), showing the salt stratification and salt wedge. From Chambers and Sparks (1959).



Concentrations of dissolved oxygen of the Houston Ship Channel in parts per million (ppm) and dissolved oxygen isopleths at 2 ppm intervals.

Fig. 30. Concentrations of dissolved oxygen of the Houston Ship Channel in parts per million and dissolved oxygen isopleth at 2 ppm intervals. From Chambers and Sparks (1959).

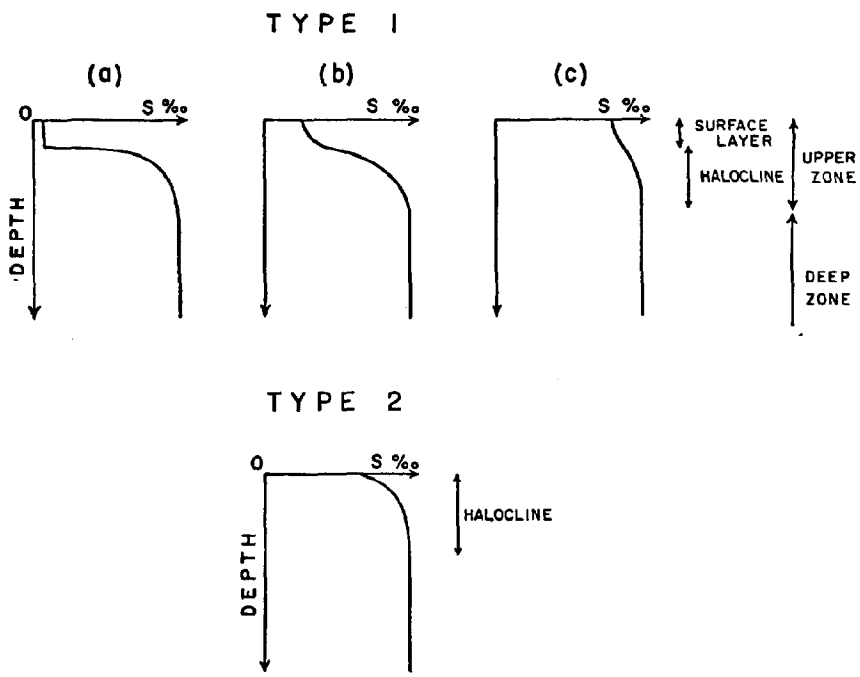


Fig. 31. Types of pycnoclines in the upper zone of some British Columbia and southeast Alaska inlets. The density is primarily controlled by the salinity, so that the increases in salinity are accompanied by proportional increases in density. From Pickard (1967).

(for example, see Figs. 8, 31). It should be pointed out that there are some tropical embayments that behave as stratified estuaries, but they receive no river run-off, their circulation is wind-driven (rather than tide and river-discharge driven), and the vertical increase in water density in them arises from the vertical distribution of heat. In these systems, there is an intermediate depth zone in which the temperature decreases relatively rapidly with depth (the thermocline), giving rise to a thermally-induced pycnocline. The example cited is the Gulf of Cariaco, on the north coast of Venezuela (Figs. 23, 24, 25) (Richards, 1960; Gade, 1961).

Estuarine Circulation

The river water entering the head of an estuary is less dense than the water below and tends to float on it. However, as it travels toward the sea, the river water mixes with the salt water; during this process, the salt content of the upper layer increases, so that salt is carried seaward in the upper layer. To replace this salt and to maintain continuity, new seawater enters the mouth of the estuary. Thus, there is outward flow at the surface and inward flow at depth at the mouth of the estuary (Figs. 21, 32). This is a characteristic flow pattern in estuarine basins; these conditions are common in fjord basins in temperate latitudes.

The general circulation pattern described above can be modified or even reversed by the energy of the tides, the winds, or the river run-off. If strong winds blow up the estuary from the seaward end, the low-salinity layer may be thickened, the discharge of the river water through the mouth may be decreased, and the influx of saline water through the mouth may be retarded. In the opposite case, the outward flow of the river water may be hastened, its vertical mixing increased, and the influx of seawater increased.

Flushing

The sea outside the mouth of the estuary may be considered an infinite source of saltwater, the density of which may fluctuate seasonally or may be relatively constant; in any case, the density of the seawater that can enter the estuary is controlled by the depth of the sill and the vertical distribution of density in the water column. The fate of that water after it enters the estuary depends on the density distribution in the fjord basin. If the density of the water coming in over the sill is greater than that inside, the incoming water will tend to cascade downward inside the basin and in the extreme case, continually replace the deepest water with new water. An example is the water flowing into Puget Sound over the Admiralty Inlet sill (Fig. 32). In the other extreme, the incoming water may be less dense than the basin water, in which case it does not cascade to the bottom but only enters the circulation of the upper layer. This leaves the deeper waters to stagnate with ill-effects to be discussed. This condition is exemplified in Fig. 32 in Dabob Bay, where the bottom waters may remain stagnant for several months (Barnes and Collias, 1958). Intermediate cases exist, where the deeper water may be partially replaced continuously or wholly replaced seasonally or occasionally. In Saanich Inlet (Fig. 5) it appears that the deeper water of the fjord stagnates from early spring until late fall, when it is replaced by new, oxygen-bearing water, probably annually. The deep waters in Lake Nitinat are probably never entirely replaced with new, oxygenated water, but about 20% of the deeper water of the fjord was replaced between June and August, 1966.

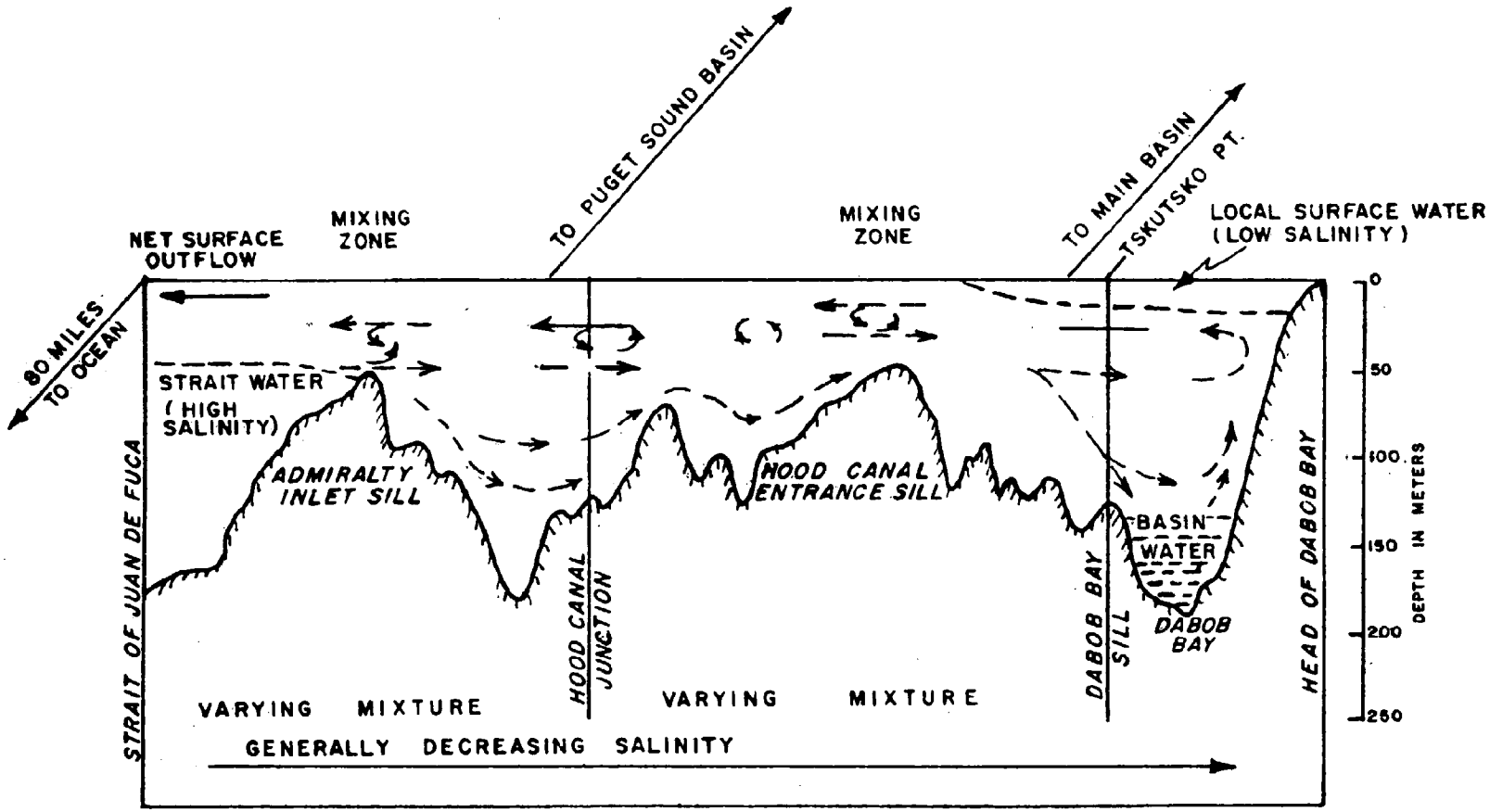


Fig. 32. Basin and sill structure on a schematic representation of water circulation in Puget Sound and the Hood Canal - Dabob Bay subsystem. The water coming over the sill into Dabob is less dense than the water in the basin of the bay, and so the basin water may stagnate for long periods. Figure courtesy of Dr. Clifford A. Barnes.

Some extreme cases exist in which the geological uplift of the land has resulted in fjords becoming landlocked. Examples are known in Norway (Strøm, 1957; 1961) and in British Columbia, Canada (Williams, Mathews, and Pickard, 1961), and there are some Alaskan systems that have not been investigated but that may be of this type. The fossil seawater remaining in the fjords has undergone drastic chemical change, and the deeper water in them contains large quantities of ammonia, hydrogen sulfide, carbonate, and bicarbonate ions. Life, other than bacteria, is excluded from them by their sulfide content. These systems probably cannot be considered to be estuaries but they are generically related.

Another system that should be mentioned is exemplified by the Lake Washington Ship Canal system in Seattle, Washington (Fig. 33). The canal, formally opened in 1917, connects Lake Washington to Lake Union and Lake Union to Puget Sound. The present level of the system is some 18 feet above the level of the sound at low tide, and a set of locks joins the canal to the sound. During periods of minimal precipitation and freshwater flow into the system, which are generally periods of the most numerous lockages, the system receives some seawater from the sound. The saltwater then flows into the deeper part of Lake Union and has, on occasion, spilled over into Lake Washington. These pockets of saltwater form highly stratified systems in which hydrogen sulfide has been observed to accumulate during the summer and early autumn. They are generally washed out during periods of heavy rainfall in the fall or early winter.

Stagnation

Stratified estuaries may stagnate, and if they do, all the dissolved oxygen may be removed from their deeper water by the respiration of plants and animals or the bacteriological decomposition of organic matter. If, after the oxygen is used up, more organic matter showers into the deeper water and decomposes, nitrate and nitrite ions are reduced to gaseous nitrogen, and then the formation of hydrogen sulfide will begin. Hydrogen sulfide is an odorous substance that is poisonous to all forms of life except certain bacteria. Its presence, even in the deeper parts of an estuary, may be objectionable because of its toxic effect on the plants and animals on the bottom and because, under certain circumstances, it may be flushed (or overturn) into the upper layers and cause a mass kill of animals, especially fish (Brongersma-Sanders, 1957). Such occurrences, although infrequent, must be considered nuisances. In some of these systems, sulfides may develop in the deeper water but never become mixed into the upper layer (although they may diffuse upward slowly, they are rapidly oxidized) and cause no particular harm, except for the absence of bottom plants and animals. Extreme cases might be encountered where so much sulfide was produced that the entire system became toxic. These conditions are probably limited to small, highly confined estuaries receiving relatively large quantities of organic matter, probably as a result of man's activity rather than by natural production.

Nutrient Traps, or Sinks, and Overfertilization

In marine waters, the ultimate amount of plant or animal life that can be formed is limited by the availability of nutrient or fertilizer elements, specifically phosphorus and nitrogen. These nutrient elements

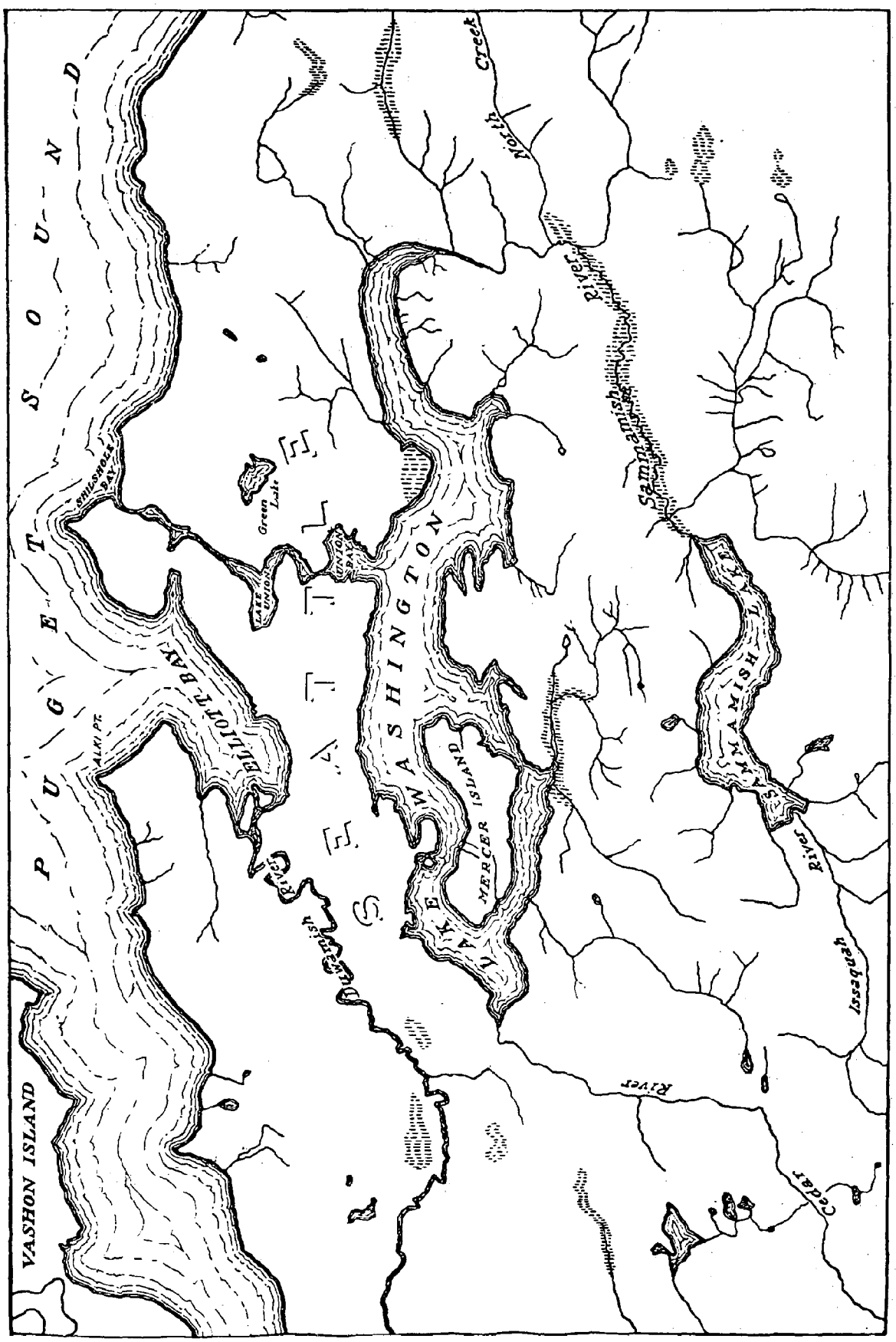


Fig. 33.

Map of the Lake Washington-Lake Union-Puget Sound system. From Smith and Thompson (1927).

are incorporated into plant material in the upper layers by photosynthesis and stripped from the water during the process. Once incorporated into the plants, the nutrients enter the food web when eaten by the zooplankton and other animals. Once incorporated into the bodies of plants and animals, the fertilizer elements are transported through the water by swimming motions and by the gravitational sinking of the dead remains of organisms and fecal particles. The net flux of this insoluble organic material (living and dead) is downward, so its decomposition returns the fertilizer elements to the deep water as inorganic solutes. This process results in a net downward transport of the nutrients, so that they are removed from the surface layers and are concentrated in the deeper water.

The nutrients can then be returned to the surface layers only by the motion of the water itself. In the open oceans and in many estuaries, water circulation and mixing prevent this process from building up relatively large concentrations of these elements, but in the stratified estuaries in which the deeper waters are stagnant, much larger than normal concentrations of these elements can accumulate. These systems have therefore been called nutrient traps. There is a natural limitation to the amounts of these elements that can build up before the dissolved oxygen is all consumed from the water; and, as pointed out above, after all the oxygen is gone, denitrification will ultimately remove all the nitrate and nitrite ions from the water. The continued decomposition of additional organic matter showering into stagnant waters results in the continued accumulation of phosphates, carbonates, and ammonia. Thus, if water from these depths is mixed with overlying water that contains enough oxygen to decompose the sulfides, the resulting mixture may be exceptionally rich in fertilizer material. If this water is introduced into the photic zone, overfertilization may be the result, and weed crops of phytoplankton may be produced. This is the process that is contributing markedly to the deterioration of the Oslofjord.

It is apparent from the above discussion that overfertilization of the stratified estuary can result from the concentrating effect of the nutrient trap. It is equally evident that this undesirable end result will be produced more rapidly if the source water of the estuary contains unusually large amounts of the fertilizer elements, as is the case when the entering water receives domestic sewage or run-off from fertilized agricultural land.

Properties of Threshold Fjord Estuaries

Several properties can be used to characterize or categorize stratified threshold fjord estuaries and predict their possible stagnation.

Depth of the sill

The depth of the sill and its relationship to the depth of the pycnocline will tend to determine whether or not the deep water of a fjord circulates. If the sill depth coincides with the depths through which the pycnocline migrates seasonally, the basin may flush annually; if it is near an extreme of the depth range of the migration, the basin may stagnate occasionally or it may flush occasionally, generally in response to climatic or meteorological extremes.

The character of the stream flow

The volume of stream flow generally varies seasonally. The greater the stream flow, the deeper to which the mixing induced by it will extend. In relatively shallow basins, this mixing may extend deep enough to flush out water that stagnates during periods of less freshwater influx, as is the case in Lake Union.

The thickness of the mixed upper layer and the depth of the interface between oxygen- and sulfide-bearing waters

The pycnocline generally deepens as the head of a stratified estuary is approached (See Fig. 8) because the mixing energy of the entering stream is more concentrated there. The depth and slope of the pycnocline will vary in response to seasonal variations in stream flow and in response to the wind.

In systems where sulfides develop, the depth of their upward limit is important in determining several of the consequences of their presence. If the sulfides extend into the depths to which light penetrates, populations of photosynthetic sulfur bacteria can develop. These may give a distinctive coloration to the water and produce free sulfur from hydrogen sulfur which in turn makes the water turbid. On the other hand, if the oxygen-sulfide interface is too deep for light to penetrate to it, the sulfide zone will be characterized by sulfate reducing bacteria.

Intensity of sulfide production

The different balances between the supply of organic matter and the circulatory removal of the products of its decomposition result in widely varying degrees of sulfide production and accumulation. For example, Saanich Inlet is characterized by maximum sulfide concentrations of 20 to 30 micromolar; in the Black Sea, maxima are around 300 micromolar; while Smith and Thompson (1927) observed concentrations of up to approximately 1000 micromolar (1 millimolar) in Lake Union in 1926. These quantitative differences are probably associated with qualitative differences. For example, Atkinson and Richards (1967) have shown that methane (marsh gas) occurs in some sulfide-bearing marine and estuarine environments, but its formation seems to lag behind the first formation of sulfides. Methane has not been observed in Saanich Inlet, although sulfide concentrations in the deep water of the inlet are about as high as those observed in the Cariaco Trench (Fig. 34), an oxygen-free basin in the Caribbean Sea (Richards and Vaccaro, 1956) in which methane does occur. The difference may be one of time; Saanich Inlet probably flushes all its oxygen-free water out each fall, but the depths of the Cariaco Trench are probably never free of sulfides.

The quality of the freshwater source

Quality is used in this sense to mean the concentrations of nutrient elements (specifically nitrogen and phosphorus) in either organic or inorganic combination in the freshwater source. Inorganic and organic forms will have somewhat the same kinds of effects on the systems, but their effects will

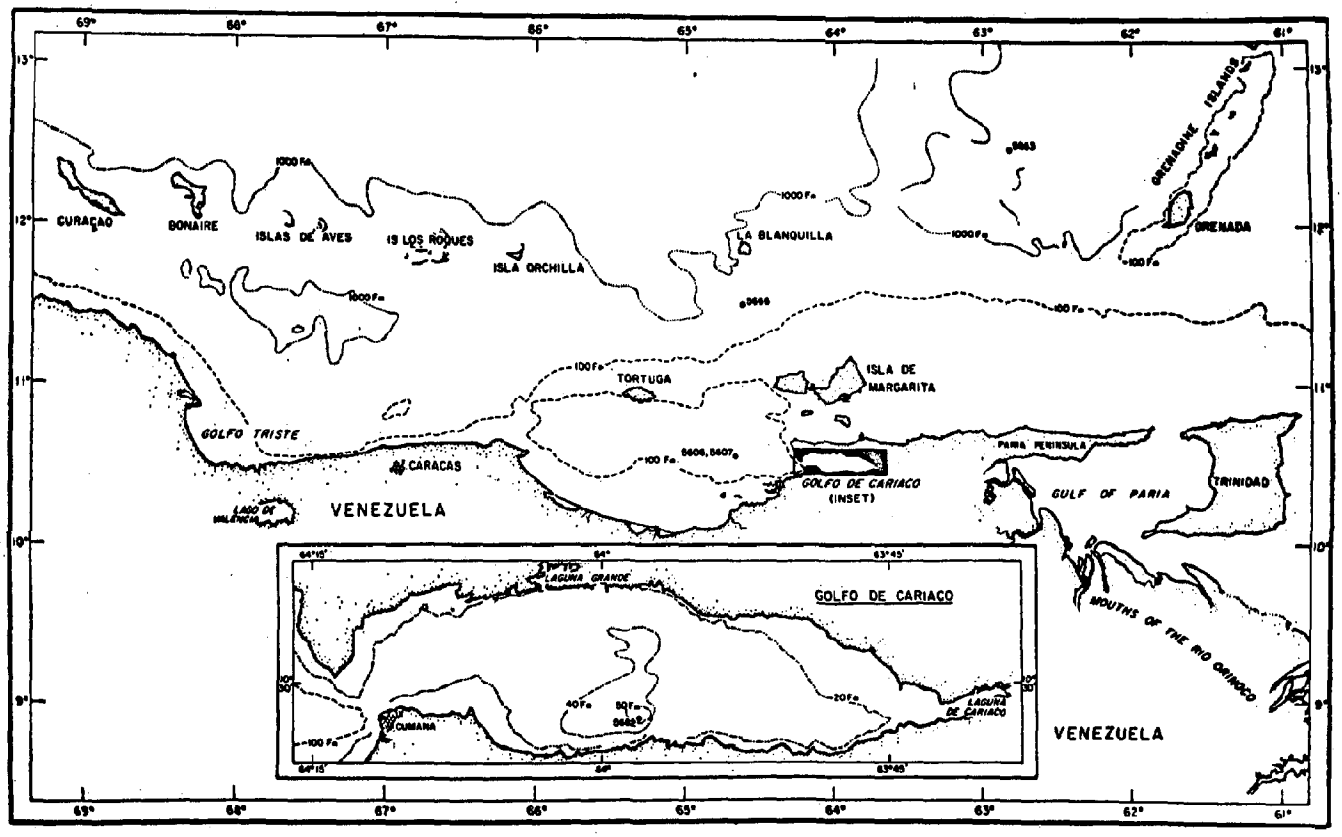
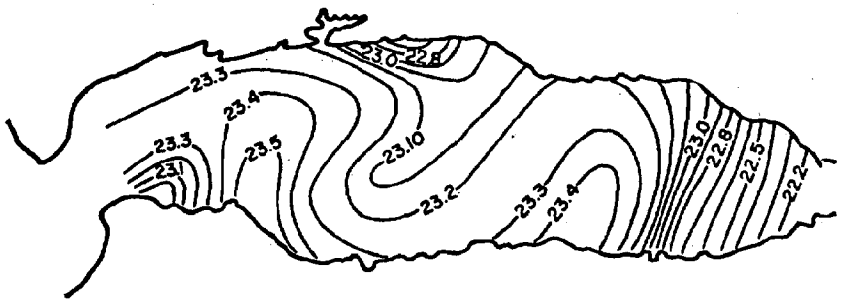
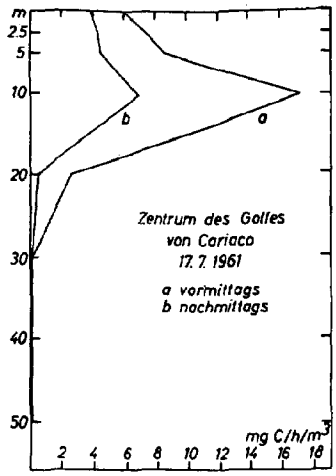


Fig. 34a. The Cariaco Trench and Gulf of Cariaco in the Caribbean Sea. These tropical systems contain deep waters that stagnate and contain hydrogen sulfide, and are similar in this respect to stagnant fjords. The Cariaco Trench always contains sulfides from 300 or 400 m to the bottom. The occurrence of sulfides in the gulf is transient, and they are occasionally flushed out (Gade, 1961) Figure from Richards (1965).

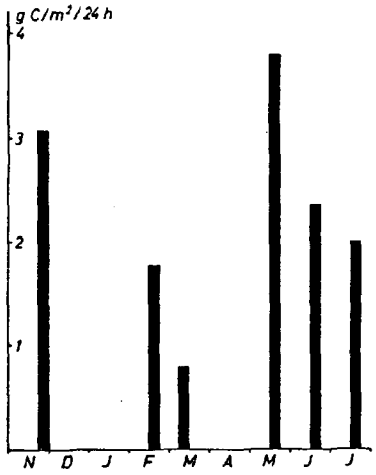


Oberflächentemperaturen im Golf von Cariaco im Mai 1961
(nach GADE 1961)

Fig. 34b. Temperatures in Gulf of Cariaco (Gessner and Hammer, 1967).



In-situ-Messungen der Primärproduktion im Golf von Cariaco,
Vor- und Nachmittagswerte



Primärproduktion des Golfes zu verschiedenen Jahreszeiten

Fig. 34c. Data on Gulf of Cariaco, a stratified tropical estuary. Photosynthetic productivity by depth above and month below (Hammer, 1967).

differ quantitatively. If the fertilizer elements are introduced in organic form, they will have a preestablished oxygen demand, whereas the inorganic forms must be incorporated into particulate matter, mainly by photosynthesis and secondarily by direct bacterial uptake, before they have an oxygen demand or can sink into the deeper layers to decompose there. Natural streams generally have moderate burdens of the fertilizer elements, in either organic or inorganic form. However, increasing numbers of streams are polluted by fertilizers, either from the drainage of agricultural land or domestic sewage. The qualitative effects of the natural and polluted stream burdens are about the same, but the quantitative differences are apt to be large.

A secondary difference will arise between the introduction of, for example, equal amounts of nitrogen and phosphorus in organic or inorganic combination. The organic residues will have an oxygen demand and on their decomposition, will introduce carbon dioxide into the water which will tend to lower the pH. Equal amounts of inorganic phosphorus and nitrogen compounds could enter the biological cycle only after being incorporated into plant cells (in general) via photosynthesis - a process that consumes carbon dioxide and raises the pH. The photosynthetic pH effect will be confined to the upper layers, but the effect of decomposition on pH will not, so the vertical distribution of pH could be expected to differ in the two cases.

The many other kinds of pollutants that are introduced by stream flow into stratified estuaries may have widely differing effects on the properties of the fjord waters. In general, as the stream meets and mixes with the seawater, the pollutant is diluted, unless it is in particulate form or is converted to particulate form, in which case it can shower into the deeper water of the basin and become concentrated. The conversion to particulate form may be by uptake by living plants or animals, by sorption on particles in the system, or by the primary formation of insoluble matter on contacting the seawater. Any of these processes will tend to concentrate the pollutant in the stagnant deeper waters.

Reducing conditions

The depletion of the dissolved oxygen in the deep water of stratified estuaries is accompanied by a gradual decrease in the oxidation potential of the water, until very low oxygen concentrations are reached. During the last stages of oxygen disappearance and in the first appearance of sulfides, the oxidation potential decreases rapidly. It then continues to decrease, but much more gradually, as the sulfide concentrations increase (Table 1).

The value of the oxidation potential in sulfide-bearing water appears to be low enough to change the oxidation state of certain metal ions, such as iron and manganese, in solution. It probably also acts to enhance the preservation of organic matter in the sediments laid down in these environments. These sediments are rich in organic matter and tend to be dark colored oozes, ranging from olive greens to black. The sediments contain a large number of organic compounds, and green chlorophyll or chlorophyll degradation products have been extracted from some of them.

TABLE 1. Redox potentials, oxygen and sulfide concentrations, and $SO_4^{=}/Cl$ ratios in the Black Sea. (After Skopintsev *et al.*, 1958 and Skopintsev, 1957; from Richards, 1965a)

REDOX POTENTIALS, OXYGEN AND SULFIDE CONCENTRATIONS, AND $SO_4^{=}/Cl$ RATIOS IN THE BLACK SEA. (FROM SKOPINTSEV[10, 20])

Depth	Redox potential (mV)	Oxygen concentration		Sulfide concentration		$SO_4^{=}/Cl$
		ml/l.	μg-at./l.	ml/l.	μg-at./l.	
0	395	5·60	498			0·1408
25	408	7·06	628			—
50	404	6·35	565			0·1418
100	340	1·08	96			0·1408
150	— 26	0·25	22	0·02	2	0·1402
200	— 88	0·08	7	0·67	60	0·1400
300	—139	0		1·74	155	0·1394
500	—170	0		3·60	320	0·1387
750	—152	0		5·29	471	0·1377
1000	—144	0		6·15	547	0·1380
1500	—129	0		7·34	653	0·1378
1750						0·1378
2000						0·1361

TABLE 2. Model relationships between oxygen consumption and the release of phosphorus, nitrogen, and carbon compounds during the decomposition of organic matter in seawater. From Richards (1965a).

MODEL RELATIONSHIPS BETWEEN OXYGEN CONSUMPTION AND THE RELEASE OF PHOSPHORUS, NITROGEN, AND CARBON COMPOUNDS DURING THE DECOMPOSITION OF ORGANIC MATTER IN SEAWATER

Atoms of oxygen consumed	Released to the water					
	$PO_4^{\equiv}$ ions	NO_3^- ions	moles N_2	moles NH_3	moles H_2S*	moles CO_2
DURING OXIDATION BY FREE O_2						
As O_2 276	1	16	—	—	—	106
DURING DENITRIFICATION						
(assuming no oxidation of NH_3)						
From NO_3^- 254·4	1	—	42·4	16	—	106
(assuming oxidation of NH_3)						
From NO_3^- 283·2	1	—	55·2	—	—	106
DURING SULFATE REDUCTION						
From $SO_4^{=}$ 212	1	—	—	16	53	106

*The total of H_2S, HS^-, and $S^=$.

The preservation of the organic matter in these environments may be, in part, the consequence of reduced oxidation potentials, but it is probably also the result of the exclusion of bottom animals from the basins. The chewing, grinding, and digestive processes of bottom animals are potent agents for decomposing organic matter and conversely, their absence would help preserve the material.

Biological populations

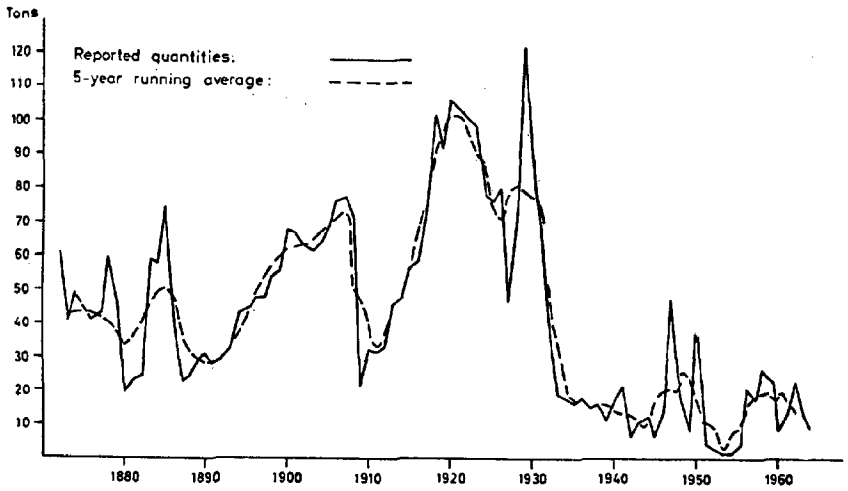
The presence of stagnant, sulfide-bearing water in the depths of threshold fjord estuaries may have little if any affect on the biological populations in the upper layers. For example, the Black Sea, which although not a fjord has many of the properties of a very large stagnant estuary, has an abundant flora and fauna in the upper layers; the sulfide zone begins 125 to 200 m below the surface, but the upper layers support some 221 algal species, and around 170 fish species. Similarly, although Lake Nitinat contains toxic concentrations of sulfides at all depths greater than about 100 m, the plant and animal life in the surface layers is little affected.

On the other hand, the deterioration of Oslofjord has been accompanied by a marked decreasing trend in fish landings since 1930 (Figs. 35, 36), and four species of fish have disappeared from the deep waters of the fjord where they were known to exist in 1897 (Ruud, 1968b).

The upper layers of stratified threshold fjords are apt to be naturally stressed systems. The regions where they occur often have high velocity tidal currents and receive much river run-off and direct precipitation. The presence or absence of a stagnating deep basin will probably have little effect on the populations in the upper layers, which should be like those of otherwise similar environments.

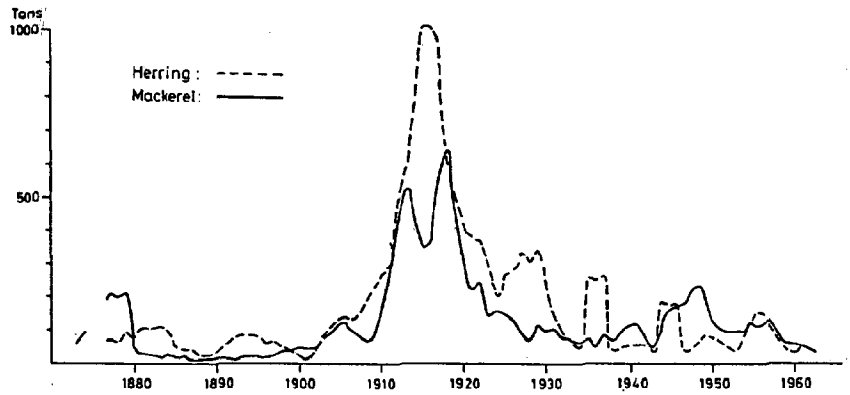
These systems become ecologically different at the point where denitrification begins. This process can begin only when oxygen concentrations reach very low (or zero) values. Denitrifying bacteria would then characterize the ecosystem. Denitrification appears to proceed in two steps in seawater: in the first, nitrate ions serve as hydrogen acceptors and nitrite ions accumulate; in the second, the nitrite ions act as hydrogen acceptors and free nitrogen is produced. Studies of these processes in Saanich Inlet and Lake Nitinat (Richards, 1965a,b; Richards, Cline, Broenkow, and Atkinson, 1965) suggest that further reduction to ammonia (or hydroxylamine) probably does not take place in the marine environment, or takes place to a limited extent. The evidence for these steps in the process are spikes of relatively high nitrite concentrations that have been observed lying over the sulfide zone in Lake Nitinat (Fig. 10) and in accumulations of greater concentrations of free nitrogen in sulfide-bearing waters than would be expected from the solution of air.

Probably different bacterial assemblages are responsible for the above two phases of denitrification. Once sulfate reduction (equivalent to hydrogen sulfide production) begins, the bacterial populations will be characterized



Annual landings of cod from the Oslofjord inside Drøbak

Fig. 35. Annual landings of cod from the Oslofjord inside Drøbak. From Ruud (1968b).



Annual landings of herring and mackerel from the Oslofjord inside Drøbak.
(3-year running averages)

Fig. 36. Annual landings of herring and mackeral from the Oslofjord inside Drøbak (3-year running averages). From Ruud (1968b).

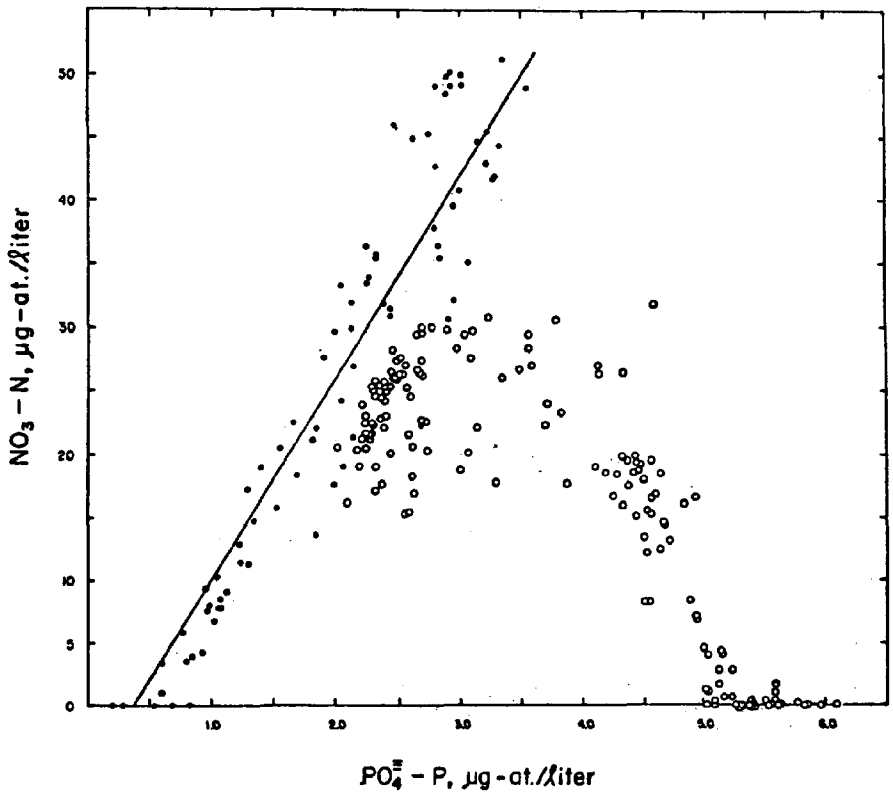
by sulfate reducers. Thus, the populations that are characteristic of stratified estuaries are nitrate, nitrite, and sulfate reducing bacteria, and these enter the scene only when all, or nearly all, of the dissolved oxygen has been consumed from the water. If sulfides are produced in or introduced into the photosynthetic zone, photosynthetic sulfur bacteria will become predominant.

The decomposition of organic matter of marine origin in natural systems is a biological-biochemical process that requires hydrogen acceptors that are reduced to lower oxidation states during the process.

While free oxygen is present in the water, it is the hydrogen acceptor of preference, but when it is all, or nearly all gone, nitrate and nitrite ions are generally the next preferred hydrogen acceptors. When they act as hydrogen acceptors, denitrification takes place, probably in two steps. During the first step, nitrate ions are reduced to nitrite ions, and there may be a buildup of unusually high nitrite concentrations. However, the decomposition of additional organic matter results in the further reduction of nitrite ions to free, molecular nitrogen. When all, or nearly all of the nitrate and nitrite ions have been reduced, sulfate ions are reduced and hydrogen sulfide is produced.

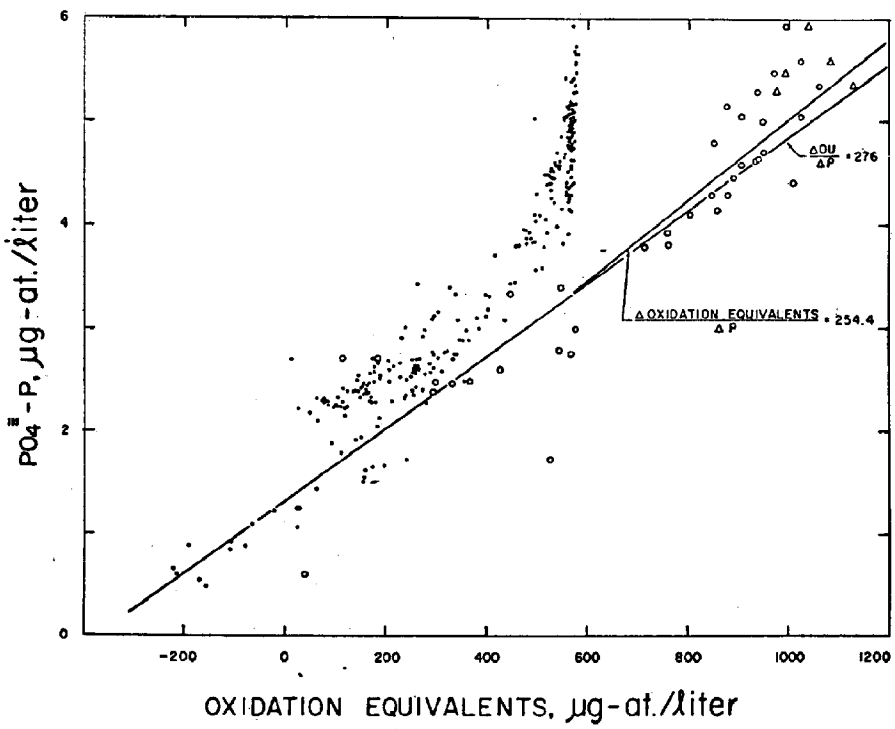
As organic matter decomposes in the marine environment, inorganic decomposition products are returned to the water. The cycles of carbon, nitrogen, sulfur, and phosphorus are of particular interest in this connection. On the average, natural organic matter of marine origin contains carbon, nitrogen, and phosphorus in the ratios of 106:16:1, by atoms. When organic matter having these atomic ratios decomposes completely, inorganic forms of carbon, nitrogen, and phosphorus are returned to the water in these ratios. These ratios are also related to the consumption of oxygen - as free, molecular oxygen while it is present in the water, then from the oxygen of nitrate, nitrite, and sulfate ions when oxygen-free conditions prevail.

In the open ocean, the concentrations of phosphate and nitrate ions in the water change in a nearly constant proportion to each other, but in Saanich Inlet, where denitrification occurs, the linear relationship is destroyed (Fig. 37). Similar linear relationships exist in the open ocean between the regeneration of nutrients and the consumption of dissolved oxygen, but these also break down in waters in which denitrification and sulfate reduction have taken place, unless the oxygen from nitrate, nitrite, and sulfate ions is taken into consideration (Fig. 38). Reasonable predictions can be made from similar considerations and a model proposed by Richards (1965a) of the ratios of changes in concentrations of phosphate and nitrate ions, and the accumulation of ammonia, hydrogen sulfide, and carbon dioxide in these environments (Table 2). Large departures from these predicted rates of change can probably be attributed to the influx of organic matter of another source, such as pollution.



Relationship between phosphate and nitrate concentrations in Saanich Inlet (○) and in the open Pacific Ocean off the coasts of Washington and Oregon (●). The observations were made in Saanich Inlet April 28, 1961, November 3, 1961, and May 4, 1962, those in the Pacific Ocean were made in July, August, and November 1961.

Fig. 37. Relationship between phosphate and nitrate concentrations in Saanich Inlet (0) and in the open Pacific Ocean off the coasts of Washington and Oregon (0). From Richards (1965a).



Phosphate vs. equivalents of oxygen consumed in Saanich Inlet.

● Oxidation equivalents equal the dissolved oxygen consumption.

○ Oxidation equivalents computed from dissolved oxygen consumption and excess free nitrogen, assumed to be produced by denitrification.

△ the same as ○ plus oxidation equivalents from sulfate reduction, estimated from observed sulfide concentrations. Observations made November 3, 1961, May 4, 1962, September 12, 1962, and December 19, 1962. The curves are those predicted by the stoichiometric model.

Fig. 38. Relationships of nutrients and decomposition substrates (Richards, 1965a).

CHARACTERISTICS OF THESE SYSTEMS THAT DEVELOP THROUGH MAN'S ACTIVITIES

The first section of this chapter has generally dealt with systems that are unpolluted or relatively unpolluted natural environments, except for Oslofjord. The impact of man's activities on them has been, so far, generally slight. It has been pointed out that several of the undesirable characteristics of stagnation may or may not develop, depending on the balance between various physical, biological, and chemical factors. There is a variety of ways in which man's activities, including the introduction of wastes, could disturb the balances existing in these systems with detrimental effects. Relatively slight natural changes can also trigger imbalances that will have the same effects.

There are two basic means by which these systems can be degenerated: by decreasing their circulation and by increasing the supply of organic matter, nutrient elements, or other pollutants to them.

Decreases in Circulation

The vertical circulation of these systems is limited by their density stratification and their horizontal circulation is limited by their geomorphology - generally by the existence of a sill. Therefore, any increase in their stratification or shoaling of the sill would be steps toward stagnation and its undesirable consequences.

Increases in stratification

The introduction of waste heat would decrease the density of the upper layers and intensify the stratification. Adequate sources of heat to bring this about might be nuclear reactors.

The introduction of more saline waters will intensify the stratification. The more saline waters could be brines from various industrial processes, such as the recovery of freshwater from seawater, or natural seawater introduced artificially. The introduction of saline water as a waste product of producing freshwater from seawater is an unlikely means of increasing the salinity of threshold fjords, because these fjords are all located in regions of relatively heavy rainfall and abundant supplies of freshwater. One chemical process that could possibly have this effect is the production of magnesium carbonate, which might be undertaken in such regions.

An example of the accidental introduction of natural seawater into a comparable system took place in Seattle, Washington. Between 1901 and 1903 the channel between Lake Union and Shilshole Bay (Fig. 33) was deepened until its bottom was below the high tide level of Puget Sound. To control the flow of water, a dam was constructed at the outlet of the lake, effectively creating an artificial threshold fjord, but in the fall of 1903 the dam washed away and a flow of seawater into the lake took place during a high tide. This sequence of events was later repeated; the dam was reconstructed but again swept away in March 1914, and a high tide introduced so much seawater into the lake that use of the lakewater by mills along the waterway had to be discontinued.

An increase in freshwater influx, as by stream diversion, could be expected to intensify the stratification unless, if of sufficient magnitude, it were to increase the turbulent mixing of the upper layer enough to have the opposite effect.

Decreases of wind mixing might increase the stratification, but it is unlikely that man-made structures are apt to have this effect.

Decreases in sill depth

One means by which deep water circulation can be decreased and stagnation can be induced is by decreasing the depth of the sill. This could be the result of any number of engineering activities.

Increases in Influxes of Pollutants

Phosphorus and nitrogen compounds are apt to be introduced by the drainage of agricultural land or as treated or untreated domestic sewage. Phosphorus, nitrogen, and potassium compounds are common agricultural fertilizers, but probably only the phosphorus and nitrogen compounds would tend to overfertilize a stratified fjord estuary. Seawater contains more than enough potassium to sustain plant growth, so plant production even in brackish waters is not likely to be stimulated by potassium additions. Evidence is developing to indicate that plant growth in North American estuaries is more apt to be limited by nitrogen deficiencs than by lack of phosphorus. Several systems are known (for example, Saanich Inlet) in which there are more than adequate supplies of phosphate to support additional plant growth, but the levels of nitrogen compounds are too low for it to take place.

There is little evidence that the addition of other plant nutrients would produce overfertilization and overgrowth in the same way as nitrogen and phosphorus. There are suggestions in the literature that silicates may limit diatom production in the open ocean, but this is not likely in estuaries. Most rivers carry concentrations of soluble silicate more than adequate to sustain additional plant life.

From the point of view of overfertilization, the effluents of biological sewage treatment plants are almost as detrimental as is raw sewage. Both materials are rich in nitrogen and phosphorus compounds. However, untreated sewage, in addition to all its obvious objectionable qualities, is richer in organic matter than are treated effluents, and so has a greater oxygen demand.

Some organic wastes may be poor in nitrogen and phosphorus compounds, and be objectionable primarily because of their oxygen demand. An example would be cellulose from lumber mills and logging operations. In the Puget Sound region, areas where this might be expected may also receive the effluents from pulp mills. These stresses are treated in another chapter.

The drainage of agricultural land and its effects have been noted above. The usual case is the simple leaching of artificial fertilizers into the streams tributary to the estuary. This represents an inefficient use of the fertilizer and an economic loss to the farmer, who could be expected to make efforts to control it, although some such loss is clearly inevitable.

Chapter C-11

KELP BEDS

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INTRODUCTION

Shallow marine waters of temperate zones of both northern and southern hemispheres are colonized by dense beds of large brown algae called kelps (Fig. 1 and Fig. 2). All kelps are placed in the Order Laminariales, displaying an alternation of phases in their life history from a large sporophyte plant to a microscopic gametophyte phase.

Kelps are the most complex of all algae with differentiation of tissues into a basal rootlike holdfast, a stem-like stipe, and one or more terminal blade (Fig. 3). A few kelps display extreme tissue specialization for internal material translocation.

Kelps have received much research attention owing to dominance in their bailiwick and to the use industry has made of their chemical constituents. Kelps are dominant wherever they grow because of their size and growth habit. Several kelps are repent in the water owing to a flaccid stipe (Laminaria, Alaria), but a few are erect owing either to a woody-like stipe (Pterygophora) or to pneumatocysts (bladders) which buoy the photosynthetic apparatus to the water surface (Macrocystis, Nereocystis).

The large often spreading holdfasts of kelps exclude from attachment many organisms directly to the bottom, but compensate by providing a vertical substrate (the stipe) upward into a better lighted water layer. Shading by the canopy producing kelps, Macrocystis and Nereocystis, has a major effect of exclusion on certain benthic plants at their base. This is somewhat alleviated in the Nereocystis system by the annual habit, in which plants die and float away each year. This allows increased light to reach the bottom during the winter and allows seasonal pulses of benthic plants. The latter situation is conditioned by the energy loss in a local system when large amounts of the dominant organism and its epiphytes are exported to accumulate as drift on a beach or to sink in deep water.

The history of personal or corporate use of kelps extends back many years. Probably the earliest use of kelp was as cattle feed and fertilizers. Some early uses in this country developed as chemical tests displayed profitable levels of potassium, potash, acetone for ammunition, and iodine. The most recent use has been for algin, now used in a myriad of commercial products.

DISTRIBUTION OF KELP SYSTEMS

A number of kelps occur in the temperate zones of the northern and southern hemispheres. On the Atlantic coast of North America kelp growth

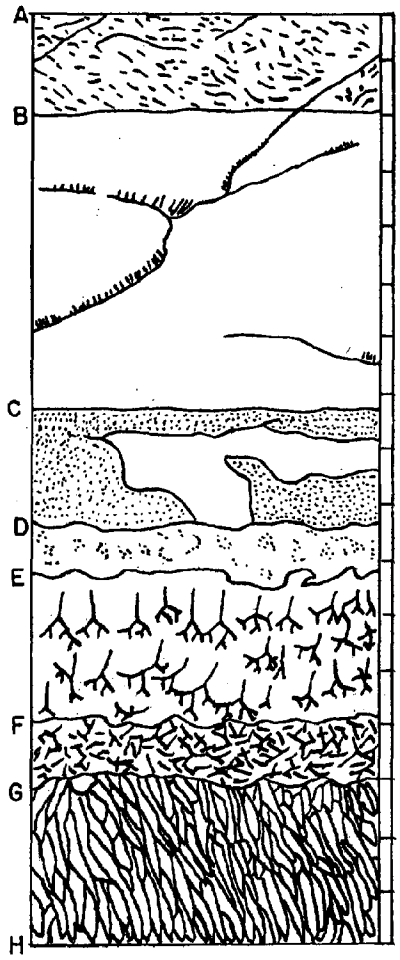

Fig. 1. Zonation at Peggy Cove, open Atlantic coast of Nova Scotia. AB - land lichens, herbs, grass, and bushes; BC - almost bare rock; CD - discolored rock with patches of blue-green algae; DE - barnacles; EF - fucoid zone; FG - Chondrus zone; GH - laminarian zone. A scale in feet on the right of the column is calculated. (After Stephenson and Stephenson, 1954).

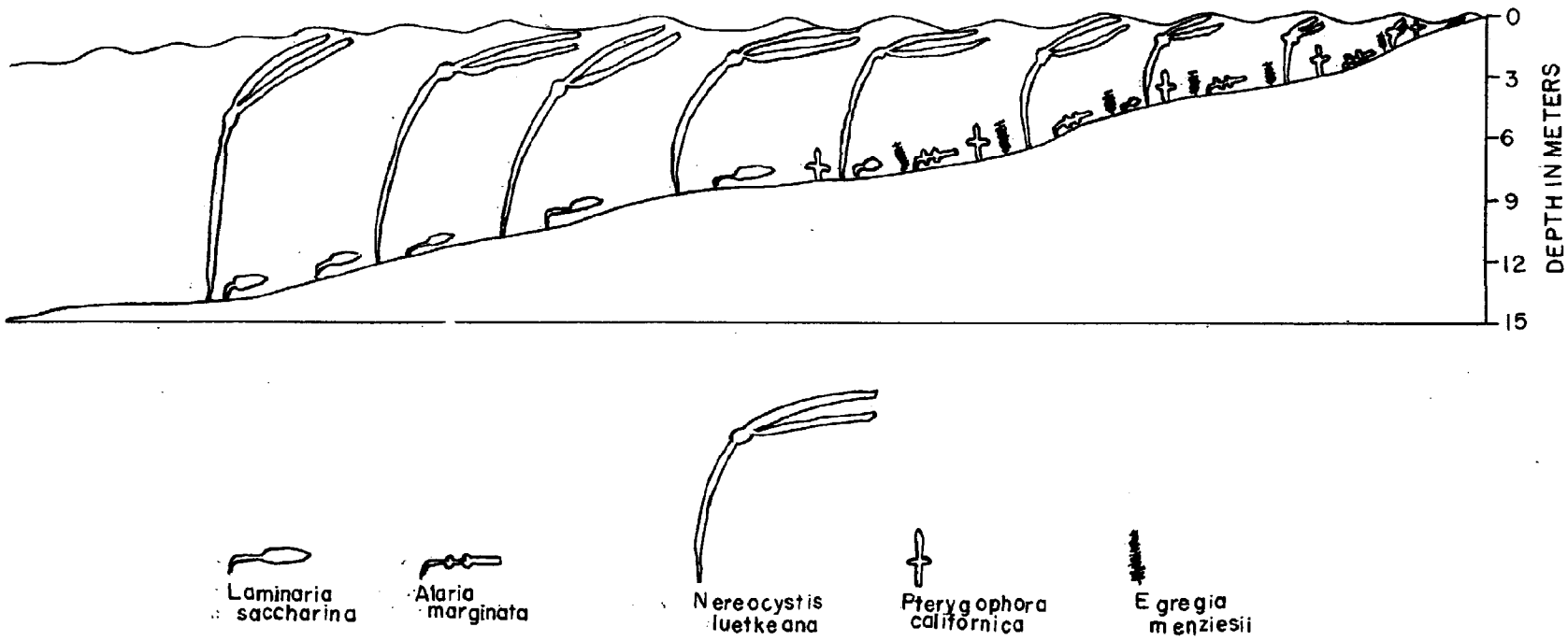

Fig. 2. Diagram of a 'typical' kelp bed in the Puget Sound area. The horizontal axis is not to scale. No attempt was made to accurately diagram the true plant density or to show all the kelps which might be present. No red algal undergrowth is designated.

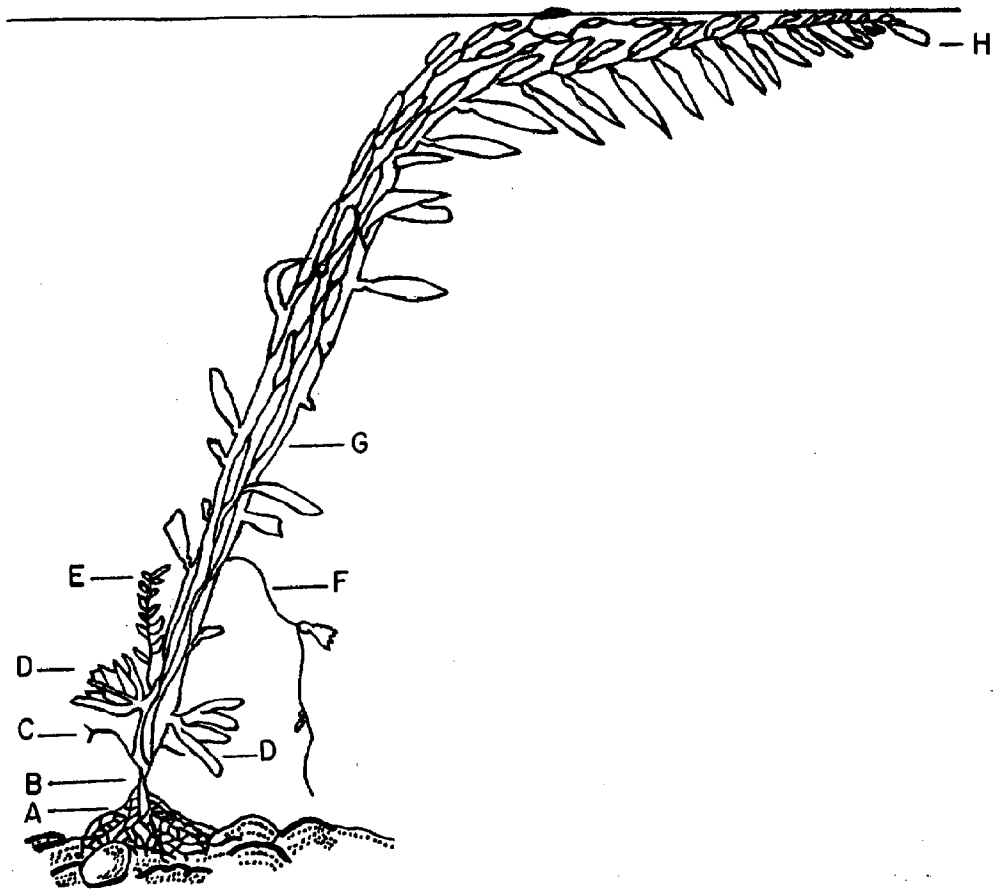

Fig. 3. Giant Kelp. Diagram of an adult kelp plant. A) Holdfast; B) Primary stipes; C) Stubs remaining from original two fronds; D) Sporophylls (reproductive blades); E) Developing young frond; F) Deteriorating senile frond; G) Bundle of stipes; H) Growing point of a mature frond in the canopy at the surface. (After North, 1960b).

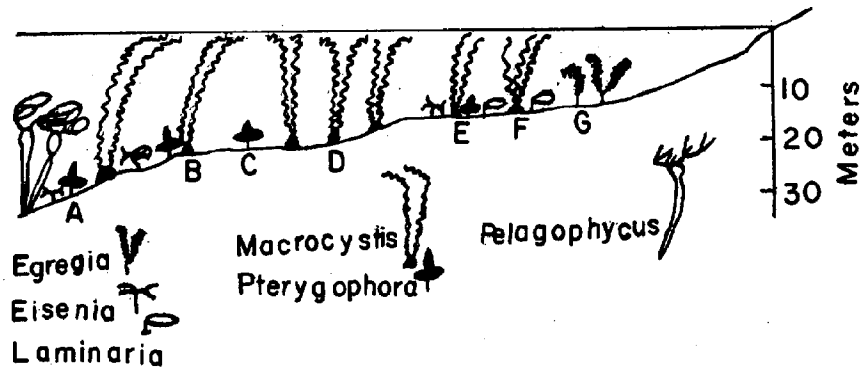

Fig. 5. Diagrammatic cross section of the kelp bed at La Jolla, California. The more conspicuous large brown algae are shown. Smaller plants forming the bottom growth were observed and collected at points A through G. The number of genera represented are as follows: A. 11. B. 6. C. 6. In the dense shade at point D. 3. E. 8. F. 8. G. 13. The horizontal scale is greatly compressed, the total distance covered by the transect being slightly over one statute mile. (After Dawson, Neushul, and Wildman, 1960).

comes to maturity in four to five months with a life span of six months. Clendenning (1960d) reported that rates of elongation of stipes in the canopy are commonly 50 cm./day or 10-15 feet/week. This is nearly twice the growth rate of bamboo (30 cm./day), which was the highest growth rate on record. Thus, giant kelp fronds near the surface possess the highest growth rate on record. Holdfasts on older plants may become several meters wide (North, 1964b), but are usually no more than one meter wide.

Flattened blades occur along the length of the stipes, but tend to be clustered at the upper apical end of the stipes owing to development by successive splitting of a primary blade at the stipe apex. Thus clustering of blades forms an apical canopy. North (1967b) noted that up to 65% of the total weight of the plant may reside in the canopy in the upper four feet of water at the surface. This depth is considered as harvesters are allowed to cut plants to a depth of four feet. Stipes and blades are buoyed to the surface by the development of pneumatocysts at the base of each blade.

Young reproductive spore-bearing blades, sporophylls, are produced at the base of the plant just above the holdfast. Energy for new growth at the plant base appears to come from food translocated downward from above by specialized sieve filaments inside the stipe.

Giant kelp normally grows on rocky substrates where currents are moderate, but where wave shock is not extreme. In the vicinity of Santa Barbara, California, large plants are found on sandy or muddy surfaces. Dense beds of kelp form an effective offshore breakwater and damp wave action inshore. Thus, they significantly reduce inshore erosion.

Geographical Distribution

Giant kelp is circum-subantarctic, on most subantarctic islands, between 40 - 60° S. Lat. (Womersley, 1954). In South America the species extends up the west coast to Callao, Peru; on the east coast attached plants are known to about 50° S. Lat., but drifting specimens have been found to the Rio de la Plata (near Buenos Aires). In North America the species occurs from 27° N. Lat., (west coast of Baja California; Dawson, 1951) to the Monterey Peninsula. Plants occur on the east and southeast coasts of Tasmania, and on the east and south coasts of South Island and near Wellington on the North Island in New Zealand. Womersley (1954) also diagrammed occurrence at the Falkland Island, South Georgia, Tristan de Cunha Group, Prince Edward Islands, Crozet Islands, and the Kerguelen Islands (Fig. 6).

Giant kelp tolerates a temperature range from close to zero in the subantarctic in winter to about 18°C. in California (Womersley, 1954). When water temperatures warm above 18 - 20°C. plants are harmed and deterioration begins (North, 1960b, c). He also stated that the degree of damage was directly related to the duration of the warm water. North (1960c) found that entire beds quickly deteriorated at temperatures of 24°C. or greater.

The report by the California State Water Quality Control Board (1964) stated that giant kelp was not harmed by salinity changes 25% higher or lower than natural sea water. After five day incubations at 20°C., photosynthetic capacities

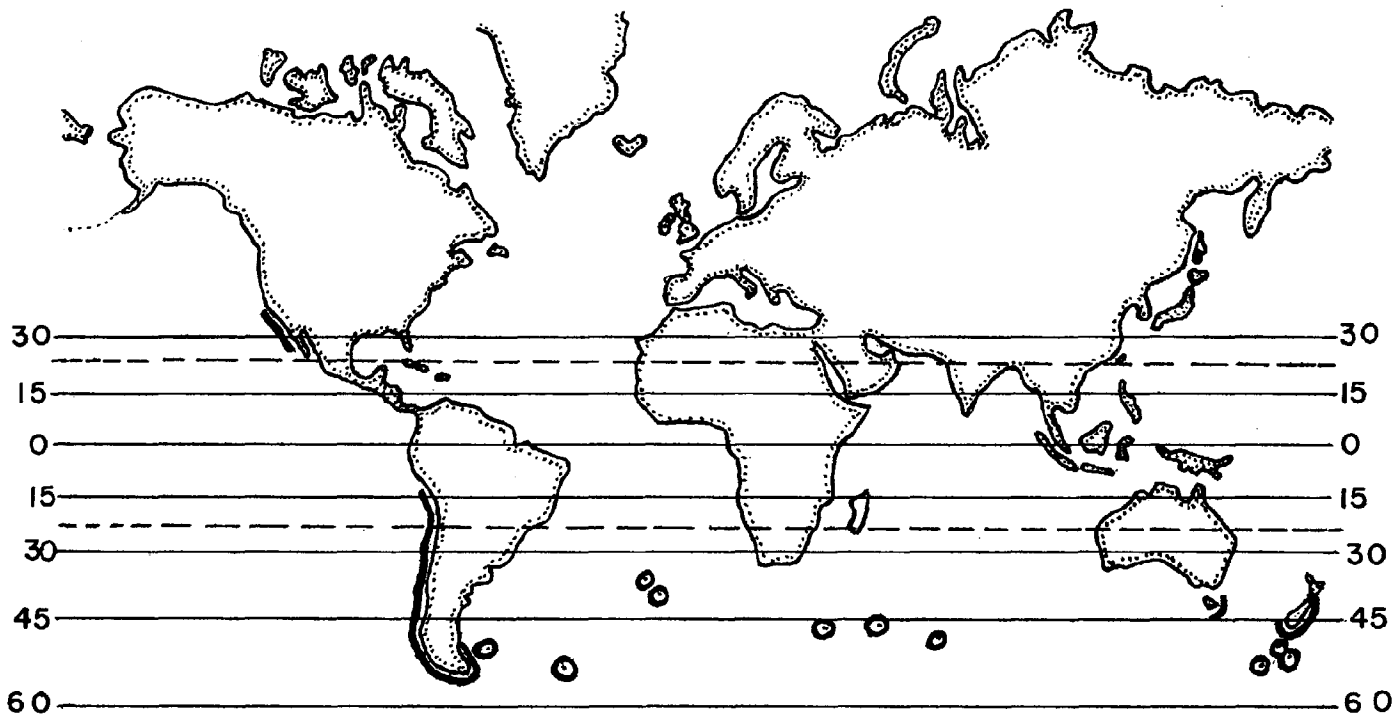

Fig. 6. World map with distribution of the Giant Kelp. Note discontinuity of distribution, extending north of equator in California. Distribution depicted as a black heavy line. (After Womersley, 1954).

of bottom fronds were reduced by 55% in sea water diluted 25%, while no reduction was seen in surface fronds. It is possible that the bottom fronds may have suffered from inimical temperatures alone.

The discontinuity in distribution from Peru in South America to 27° N. Lat. on Baja California is curious. The reason usually given as to why the species can live north of the equator is the presence of masses of upwelling cold water along the California coast. I have not encountered an explanation as to why the discontinuity exists. The cold water of the Humboldt Current along the west coast of South America is undoubtedly the reason why the species occurs north of the Tropic of Capricorn in South America.

The species probably has at least two means of distribution available: a. Zoospores liberated into the water later settle and grow into filamentous gametophytes, and b. Whole plants or their parts may float away (if the pneumatocysts are intact) and later either colonize a new area or release zoospores in a new area.

Vertical Patterns

Light appears to have the greatest influence on this pattern. Neushul (1957) stated that light was apparently one of the chief factors determining the structure and components of the kelp bed. Dawson, Neushel, and Wildman (1960) reported six species of benthic algae under a dense kelp canopy, but 28 species under an open canopy. North (1964b) found that standing crops of plants were seven times greater outside the kelp cover than inside it (excluding the giant kelp). If giant kelp were included the standing crop was three to four times greater inside the bed. North (1964b) reported that canopies of giant kelp could achieve sufficient density to reduce light intensities beneath by a hundredfold. Dawson et al. (1960) stated that available light on the bottom was less than 0.1% of the intensity just below the surface under a dense canopy. McFarland and Prescott (1959) found 40 - 50% subsurface transmission for white light at five to six cm. depth under thick canopies, while zero per cent transmission was recorded at one meter just below the canopy. They also stated that the shading capacity of the canopy was equal to that of a tropical rain forest.

Depth limits of growth in California were reported from three meters (McFarland and Prescott, 1959) to 37.5 meters (California Dept. of Fish and Game). North (1964b) stated that giant kelp was most common from 8 - 25 meters or more. North (1960c) observed that the inner limits are often determined by wave shock, while outer limits are frequently set by water clarity.

Chapman (1962a) stated that plants in California occurred at 40 - 70 feet in turbid water, but at 90 - 100 feet or more in clearer waters. North (1960b) reported that adult plants are normally fairly immune to changes in water clarity because of the high canopy, but that if the canopy were damaged by waters warmer than 20°C., storms, or grazers, changes in clarity could then affect the health of a bed by decreasing the capacity to regenerate the canopy and by slowing the growth and development of young plants. North (1967b) found that compensation levels for clear coastal waters lie between 30 - 35 meters in depth.

Neushul (1959a) determined that the 'growth compensation point' for young single- and four-bladed plants at 15°C. was between 32 - 64 foot candles of

white light, with saturation for growth around 125 foot candles. Clendenning and Sargent (1957) found that compensation (where photosynthesis balances respiration) in giant kelp was 15 foot candles of white light at 15°C. (mature blades from surface canopy). They also reported that first evidences of saturation appeared at about 400 f.c., with saturation at 1600 f.c. (Fig. 16). No reduction in photosynthetic capacity occurred at higher intensities. It was also found that the photosynthetic capacity of giant kelp varied seasonally, with the temperature, with the geographical source of the plant, and with the type and age of the tissue (North, 1958a). Clendenning and Sargent (1957) also reported that the photosynthetic capacity underwent adaptive changes as the light intensity changed. They found that the capacity of blades of young stipes near the base of the plant was half that of surface blades, and that the capacity slowly declined in surface blades when maintained at low light intensity in the ocean or in the laboratory. They found that the rate of photosynthesis at a depth of 50 feet in clear water was 30% less than the maximum rate in the surface six feet of water. However, Anderson (1967a) noted that in young bottom fronds light saturation levels were much lower than in surface blades. Anderson (1967a) recently worked out the photosynthetic action spectrum for young giant kelp sporophytes (Fig. 7). North (1958a) illustrated the relative photosynthesis in waters of different absorption coefficients (Fig. 8).

Work done by North and associates established that many aspects of growth and development of giant kelp are correlated with light. Clendenning (1960c) found that frond weight did not change with water depth, but that stipe internode length did change. Anderson (1967a) found that a bloom of sporophytes appeared in early spring times with the seasonal increase of light levels on the bottom. Neushul (1957) reported that light greatly modified the growth rates in young plants. North (1967c) concluded that lower light intensities from November to February might limit development of juvenile kelp from 9 - 12 meters. He found no juvenile plants under very dense canopies. North (1966) reported that a tremendous bloom of juvenile sporophytes occurs in the spring. Anderson (1967a) stated that light may limit kelp reproduction during certain times of the year. Anderson and North (1966a) determined that the color of light determined the shape of gametophytes. Under blue and white light gametophytes were filamentous; they were ellipsoidal or round in green, amber, or red light.

Anderson and North (1966a) stated that the intensity of red light needed for slow but definite growth of giant kelp gametophytes was near 500 ergs/cm^2/sec. for 12 hours; this was also the requirement for blue light. For green and yellow light the requirement was around 2000 ergs/cm^2/sec. North (1968g) stated that the threshold values for orange light was three times greater than for blue light, and that the violet threshold was equal to or less than that for blue. He assumed that the threshold for the total energy value for the appearance of juvenile sporophytes was less than twice the blue threshold (10^8 ergs/cm^2/day, a value above compensation).

One of the serious effects of pollution is the reduction of water clarity. North (1958a) calculated that for a young kelp plant attached in 15 meters in water with an absorption coefficient of 15%, an increase in the coefficient of 1% would reduce net photosynthesis 20% which could lead to loss of the plant, placing a higher survival pressure on more shallow plants under the influence

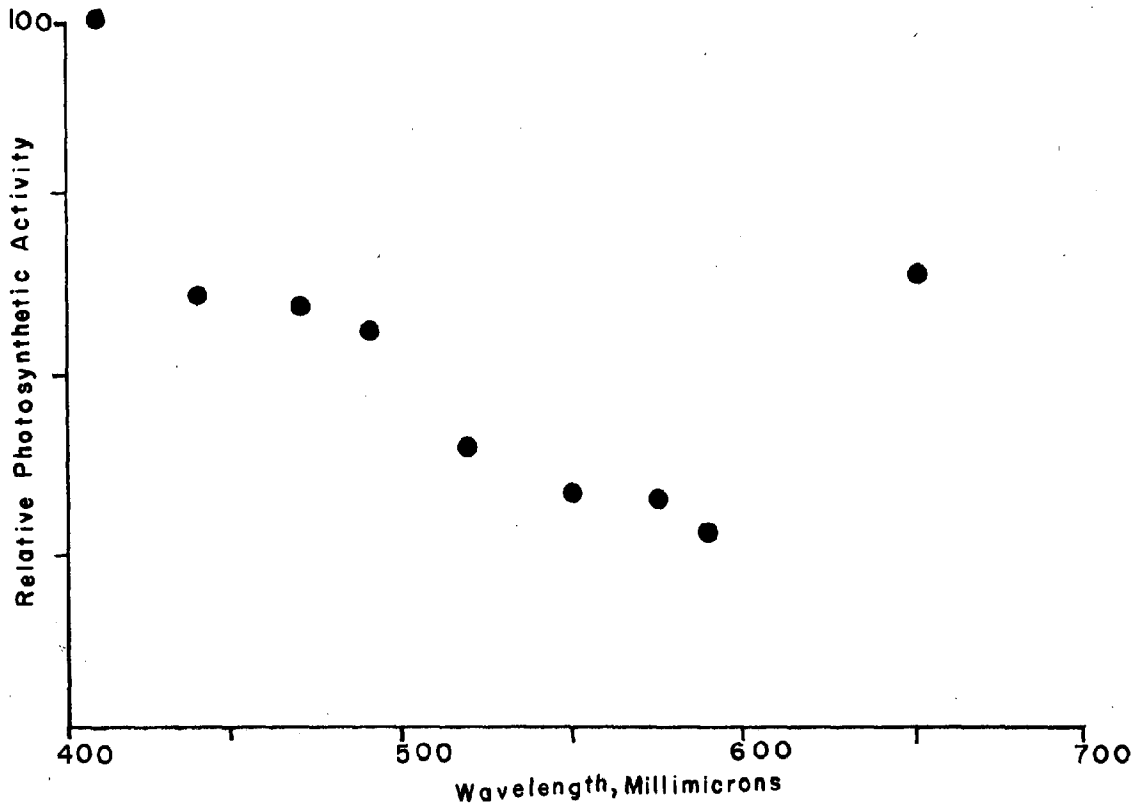

Fig. 7. Photosynthetic action spectrum of young giant kelp sporophytes. (After Anderson, 1967a).

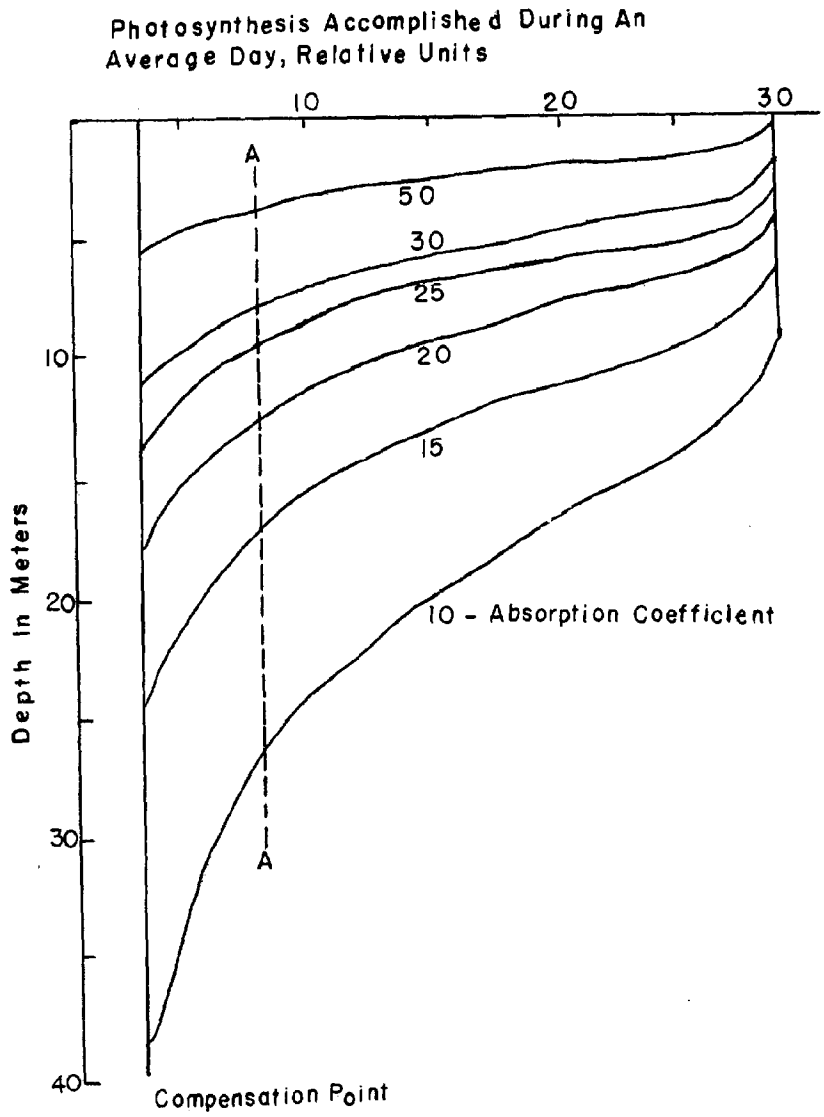

Fig. 8. Curves showing the theoretical photosynthesis at different depths of Macrocystis blades. Curves were determined for waters of different absorption coefficients. Portions of curves lying to the right of AA are regions experiencing light energies greater than 600 foot-candles for varying periods. (After North, 1958).

of grazers. Thus, the development of a massive canopy is a great advantage in turbid waters, and probably is the reason for the dominance of giant kelp as a system.

Temporal Patterns

Two types of patterns will be discussed. The first will describe seasonal patterns of development concerning vegetative and reproductive states. The second type will deal with short term growth rates.

Seasonal patterns

Fig. 9 illustrates the life history of giant kelp.

North (1964b) discussed the periodicity of succession from 'seral' stages to the climax community dominated by giant kelp. Several natural factors affect giant kelp, which then affect the regularity of this periodicity. Elevated water temperatures, storms, grazing animals, encrusting animals (the most common one was Membranipora serrilamella, a bryozoan), black rot (bacterial disease which softens canopy tissues) and another infection which softens stipe tissues hasten the demise of kelp fronds.

Basically, giant kelp is a perennial. Holdfasts constantly replace senile fronds with new ones. North (1961) found that the maximum age of individual fronds under favorable conditions in 20 meters of water was about six months, possibly extending to eight or nine months under the best growing conditions, with an average age of only two to three months. Life spans were found to vary widely according to exposure to the inimical conditions listed above.

Succession toward the climax begins with establishment of juvenile sporophyte among benthic algae. Gradually the kelp grows, forming a canopy which then shades out the vegetation underneath. As grazers or other factors eliminate kelp plants or even whole beds, benthic vegetation recolonized the relatively bare substrate. The time required for completion of the cycle of succession varied from one bed to another (North, 1964b). North reported a short cycle of two years for one bed in Mexico. Kelp beds at Santa Barbara, California, were noted to have a long cycle of about 17 years. The absence of severe grazing, warm water, and storms probably explained the low plant mortalities in the latter area (North, 1964b).

Time spans for development of gametophytes in the field have been recorded. North (1965b) found a span of about 80 days for completion of the microscopic stages in the summer of 1963, as against a span of 130 days for the same stages in winter 1964-1965. The 50% increase in time was attributed to the shorter day lengths in winter. Thus, light seems to influence the development and maturation of gametophytes. This appears to correlate with a report by North (1966) that following two weeks of very clear water at La Jolla, California, in winter 1966 tremendous numbers of juvenile kelp plants appeared in early spring. North (1968g) observed that juvenile sporophytes were very scarce in winter months. North (1966) reported that kelp microscopic stages can survive in the field for more than a year under conditions unfavorable to young sporophytes. He noted that this undoubtedly conferred survival advantage to the species. North (1968f) calculated that the life history of giant kelp in shallow water and good illumination at Turtle Bay, Baja California, was completed in less than a year (Fig.9).

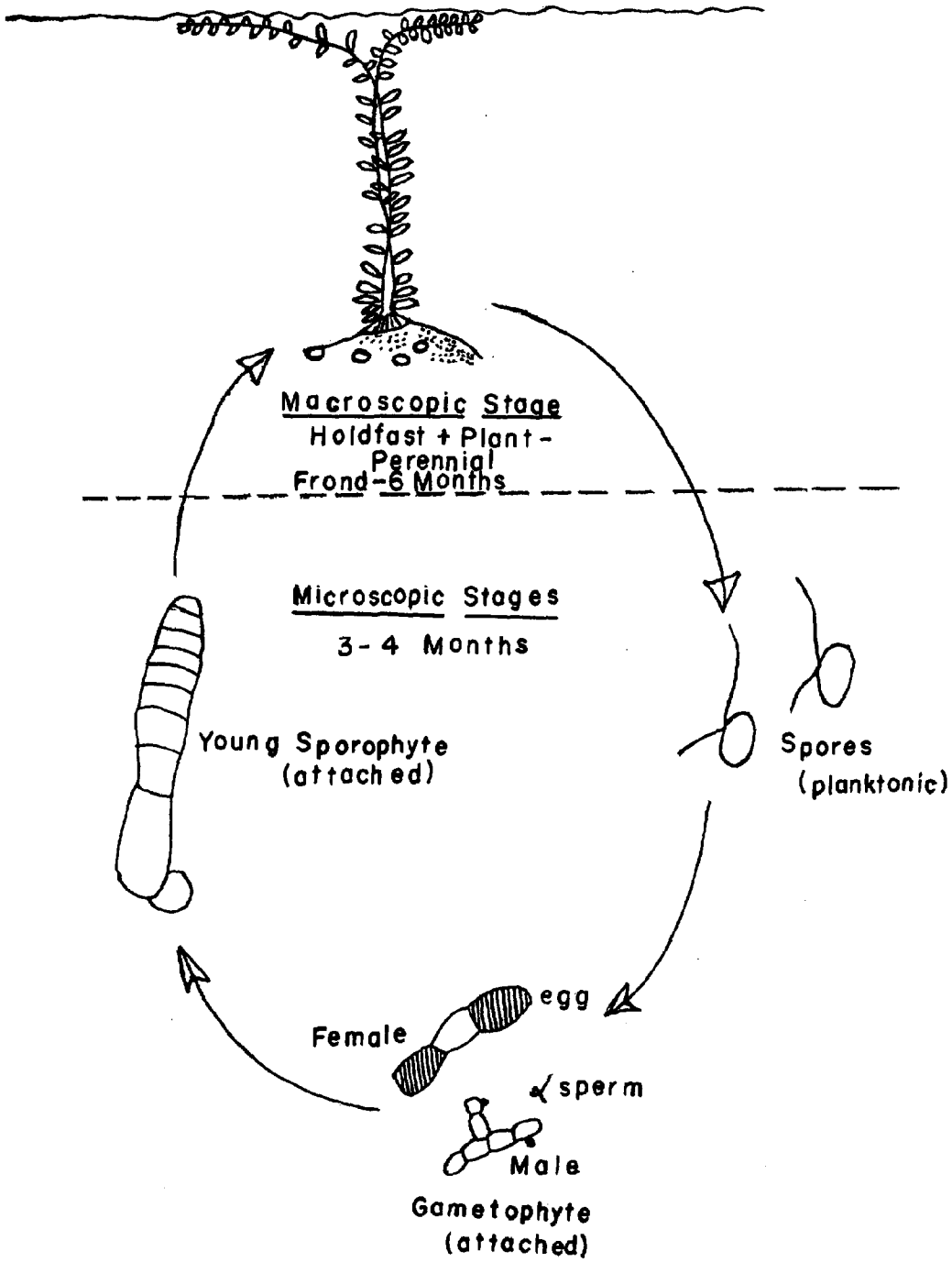

Fig. 9. Life history of giant kelp. (Adapted from Neushul, 1957). Time periods are averages from field observations. Life history span less than one year.

Neushul and Haxo (1968) reported that the minimum time needed for the completion of the life history in the sea was 12-14 months.

Anderson and North (1967) stated that two seasonal peaks of zoospore release may occur in the field, the greatest release rate appearing in late spring and early summer, with a smaller peak occurring in autumn and early winter. Spores are produced all year long by mature plants. Anderson (1967b) correlated these peaks with a peak of maximum insolation in June and a point of minimum insolation in January (when spore release was the least).

Anderson and North (1967) found that reproductive maturity of a plant was attained at an age of nine to twelve months. Neushul (1958) found that plants in the field produced spores at an age of seven to eight months.

Anderson (1968) stated that spore release rates ranged from zero to about 114,000 spores/min. cm^2 of sporophyll area. He found variation not only according to location and time of sampling, but also among plants and among sporophylls on the same plant sampled on the same day. No correlation in release rates were made with plant size, age, or depth, but a marked seasonal rate of release was observed (see above). Anderson and North (1966b) calculated average liberation rates as 3800 spores/min. cm^2 of sporophyll surface. Mean annual values for normal healthy beds ranged from 1000 - 5000 spores/min./cm^2 (Anderson and North, 1967). Boney (1966) related that one cm^2 of sporophyll could produce 69,376,000 zoospores. Considering the large area of the basal clump of sporophylls (26 g./kg. of frond; area mean 0.36m^2/m^2 of bottom; Neushul, 1959b), it is no wonder that giant kelp is considered as a primary producer of planktonic material (Neushul, 1957).

Short term growth rates

Neushul (1958) stated that many assumptions must be made when comparing growth rates of giant kelp. Very little data explained variations observed in the rate, either seasonally or in relation to specific environmental factors.

Neushul (1958) calculated from Brandt's (1923) data that fronds doubled in length every 41 days. Extreme range in doubling time of length has been reported as 10 - 68 days. Young transplanted kelp doubled in length in 14 - 24 days and in area every 20 - 30 days (Neushul, 1959a). Neushul (1957) found that plants at a depth of 50 feet in open water doubled in size approximately every three weeks. Clendenning (1960d) reported that elongation rates for giant kelp fronds were commonly 50 cm./day or 10 - 15 feet/week. He added that this was the greatest rate of elongation on record for any plant. Sargent and Lantrip (1952) reported rates of frond elongation of 7.1 cm./day (standard deviation of $\pm$ 4.3 cm.), but this was based on excised frond tips. Neushul (1957) observed from weight increments that giant kelp plants doubled every 24 days.

North (1960a) measured growth as percent increase in stipe length per day. The range in plants in 65 feet of water at La Jolla, California, was 4.5 - 19.6%, with most of the observations falling between 7.5 - 8.9% per day.

It would appear that seasonal and environmental data relating to growth are still lacking. Such experiments, if kept free of grazers, would be useful.

Principal Inputs and Outputs of Material and Energy

North (1960c) stated that in earlier years giant kelp covered more than 100 square miles (256 km.^{2}) in California. Beds presently are only one-half to three-fourths as large (North, 1968c). North (1959) calculated a conservative estimate of the total standing crop of giant kelp in southern California as about two million tons (1.8×10^9 kg.). North (1964b) diagrammed a standing crop range of giant kelp beds of 4 - 12 kg./m^2. I assume this is wet weight.

Clendenning (1960c) reported that the average standing crop was 6.6 kg./m^2 with an extreme range of 2 - 14 kg./m^2. Over half of all observations recorded 4.5 - 9 kg./m^2 of bottom area. He also reported an average 4.4 fronds/m^2 of bottom with an extreme range of 1.9 - 9.5 fronds/m^2. He stated that frond surfaces exposed averaged 15 m^2/m^2 of bottom with an extreme range of 4 - 40 m^2/m^2 of bottom.

Aleem (1956) reported a standing crop range at La Jolla of 5.64 - 9.00 kg./m^2 (average fresh weight). McFarland and Prescott (1959) found that standing stocks varied slightly with depth: a. Six meters - 4.35 kg./m^2, b. Nine meters - 5.78 kg./m^2, c. Twelve meters - 5.44 kg./m^2 (fresh wet weight). They stated that 25 - 43% of the biomass was found in the canopy. North (1967b) stated that up to 65% of the biomass could be found in the canopy. Converting stipe indices reported by North (1957) for Paradise Cove plants, McFarland and Prescott (1959) obtained values of 5.34, 5.34, and 4.0 kg./m^2 (wet weight) respectively. Leighton and Jones (1968) reported that giant kelp contained 15% dry matter.

Leighton and Jones (1968) calculated a caloric content of 43.6 Kcal./100 g. fresh weight for giant kelp. Thus, caloric values for the standing stock range as reported by North (1964b) are 1.74×10^3 - 5.23×10^5 Kcal./m^2. According to the total standing crop as estimated by North (1959) giant kelp in California represents a caloric value of 7.8×10^{12} Kcal.

Leighton and Jones (1968) found that of the 15% dry matter in giant kelp, 67% was organic material. Of this percentage, 12% was ash-free protein, 3% was lipid, and 85% was carbohydrate.

Giant kelp influences standing stocks of undergrowth. A report by the California State Water Quality Control Board (1964) stated that the mean amount of plant undergrowth under a dense canopy was 469 g./m^2, while that not under a canopy was 3145 g./m^2. Aleem (1956) found 2.49 kg./m^2 of undergrowth in seven meters, while in 15 meters, wet standing crop was 1.97 kg./m^2. In the Paradise Cove beds McFarland and Prescott (1959) found that undergrowth ranged from 0.02 kg./m^2 to 0.5 kg./m^2, with an average of 0.1 kg./m^2. North (1964) compared standing crops of attached biota at two locations, one under a giant kelp canopy, the other not under a canopy (Table 1).

There are several fates for giant kelp. Some is harvested by man, some is released and accumulated on the shore as drift or in deep water, and much is devoured by grazers.

Zobell (1959a) stated that as late as 1917-1918 more than one million tons of kelp were harvested in southern California. North (1964b) estimated that recent annual harvest amounts range between 100,000 to 150,000 tons of fresh wet weight. Clendenning (1960b) estimated that the harvest averages about 15% of the total stock. Thus, man drains a considerable amount of energy from the

TABLE 1. COMPARISON OF THE STANDING CROPS OF THE CHIEF ATTACHED PLANTS AND SESSILE ANIMALS FROM TWO LOCATIONS SEPARATED BY ABOUT 30 m FROM EACH OTHER. One site was well beneath a dense *Macrocystis* canopy, which had been in existence for approximately a year, while the other site extended out from the edge of the canopy and was free from any shading effects. Mean values, ranges, and frequencies were computed from ten samples of area 1 m², positioned randomly within the sampled location.

Classification	Under canopy			Not under canopy			Mean not under canopy / Mean under canopy
	Frequency	Range g/m²	Mean g/m²	Frequency	Range g/m²	Mean g/m²	
Phaeophyceae							
Cystoseira	1·0	22–281	90	1·0	25–436	200	2
Egregia	0	0	0	0·1	0–4	0·4	—
Eisenia	0·1	0–22	2	0·3	343–1865	405	200
Laminaria	0·2	0–52	6	1·0	2·3–1758	539	90
Juvenile							
Macrocystis	0	0	0	0·8	P*–5·8	0·9	—
Pterygophora	1·0	0·4–517	124	0·7	163–4258	1263	10
Rhodophyceae							
Fleshy reds	0·6	0–25	6	1·0	0·5–476	222	37
Calcareous reds	1·0	114–366	209	1·0	281–940	658	3
All algae‡	1·0	285–1058	469	1·0	810–6688	3145	7
Sessile animals	1·0	193–923	508	1·0	129–999	506	1

* P=present but less than 0·1 g.
‡ Does not include adult *Macrocystis* or *Lithothamnion*. (After North, 1964).

kelp system completely from the sea. Zobell (1959a) felt that the quantity of drift kelp was diminished with modern harvesting procedures.

Zobell (1959a) calculated that 90 - 300 cubic yards of giant kelp washed ashore yearly on the beaches of San Diego County, California. He also stated that more than 90% of the drift was returned to the sea during storms or high tides. The kelp which remained on the beach decomposed or was eaten by scavengers. It was found that the plants had usually broken off near the holdfast, due to structural damage to the stipes. Limbaugh (1955), Menzies (1957), and Andrews (1945) have listed a tremendous number of invertebrates which live associated with kelp holdfasts. Some of these, especially the sea urchins Strongylocentrotus purpuratus and S. fransciscanus, feed directly on the base of the stipe. Bacterial action at the stipe base can also weaken the stipe base.

If a conservative estimate may be permitted, let me assume that a cubic yard of giant kelp washed ashore will weigh 25 kg. Thus, a range of 2,250 - 7,500 kg. of kelp washes ashore yearly on San Diego County beaches alone. Ninety percent of this is returned to the sea. Not all the kelp set loose by grazers and bacterial decomposition washes ashore. Some drifts out to sea and sinks as bryozoan encrustation decreases buoyancy (Clendenning and Sargent, 1957), or as isopods eat holes in the pneumatocyst (Wing and Clendenning, 1960). No estimate has ever been made of this amount. No estimate has been made of the quantity of drift north of San Diego County.

Grazing activity on giant kelp is severe. A report by the California State Water Quality Control Board (1964) stated that giant kelp could produce new growth equal to two to three times its own weight annually. Kelp tissue annually available as animal food thus greatly exceeded two million tons. A variety of grazers eat the plants. Some do damage far beyond the immediate site of activity. Two sea urchins are especially destructive on the kelp (Strongylocentrotus purpuratus and S. franciscanus). Their preferred site of attack is at the stipe base where the removal of a very few grams of tissue may eliminate up to 3 kg. of frond and sporophylls (Leighton, 1960c). In one experiment S. purpuratus displayed a relative preference of 81 - 85% for sporophylls and blades (Leighton, 1960b). Leighton (1960c) indicated that the urchin experiences some difficulty in ascending the stipe. Thus, sporophylls and stipes are eaten in the field. Urchin activity does maximum damage to both vegetative and reproductive tissues.

North (1964b) has reported urchin concentrations as high as 50 to over $200/m^2$, with numbers falling to one or two/m^2 in deeper zones. Leighton (1960c) counted urchins in one study with a range from 8 - $63/m^2$.

Leighton (1960c) compared the number of holdfasts and average of stipes/holdfast in an area where urchins were present with an area where urchins were absent. In the area with urchins holdfasts and stipes/holdfast ranged from 0 - $1/m^2$, while in the absence of urchins holdfasts averaged 1/2 /m^2 and stipes/holdfast averaged 2 - $3/m^2$.

Leighton (1967) calculated that S. purpuratus had a seaweed requirement of 0.2 - 1.0% of body weight/day for minimum maintenance. Leighton and Jones (1968) calculated that urchins with a fresh weight of 7.0 grams, such as observed

in the field, required 0.02 Kcal./day for maintenance alone, hence required 0.046 g. plant tissue/day to maintain each urchin. Leighton, Jones, and North (1966) expanded on these data to state that 126 - 375 g. organic matter/m^2 year were required to maintain urchins in the field. Since giant kelp only produced 78 mg. to 36 g. organic matter/m^2 year, they concluded that other sources of organic matter were used by urchins (dissolved substances, zooplankton, microorganisms, and leptopel - non-living suspended matter). They stated that on the Palos Verdes Peninsula sewage supplied 380 g. organic matter/m^2 year. They felt that sewage must be the main supplement for maintenance and increase for the high observed urchin populations in the field.

Other invertebrates and fishes eat the kelp. Except for feeding rates determined for the red abalone (Leighton, 1960c), I can find no other rates of feeding on kelp. More will be stated concerning animals feeding on kelp under Food Chains. Suffice it to say that a considerable amount of energy is exported from the kelp community each year; up to 15% is drained completely by man, an undetermined amount is exported by animals, and much is transferred by food chains. Still it seems that kelp maintains its crop unless warm water, an excessive number of storms, or pollution which seems to reduce light clarity and to support a large urchin population mitigate against the maintenance.

Clendenning (1960e) stated that the biological turn-over by giant kelp was 2.0 g. C/m^2/day, four times the rate of phytoplankton. Clendenning (1960c) found that the organic matter of giant kelp was 200 - 250 g./frond, with a turnover once in four to six months. His estimate of the annual organic production was 6.53 tons organic matter/acre year, with 50% of the examined areas falling in the range 4.5 - 9.1 tons/acre year (extreme range of 2 - 14 tons/acre year). This was three times higher than that of phytoplankton/acre of open coastal water. It was 50% higher than annual production rates for eelgrass in Denmark.

Clendenning (1960c) reported that organic productivity of giant kelp plants in moderately heavy stands was 1.5 - 2.5 g. C/m^2/day on an average yearly basis. Clendenning and Sargent (1957) listed P/R ratios under continuous saturating light at 15°C.: a. Naked stipe - 4.1, b. Pneumatocyst - 7.1, c. Sporophylls - 9.2, d. Gametophyte - 13.3, e. Terminal blade to blade 20 - 11.1, f. Blade 21 to blade 61 - 18.6, g. Blade 62 to blade 120 - 22.0. They stressed that all parts and stages of the plant above the holdfast could undergo photosynthesis and that the photosynthetic capacity of the blades increased with increasing distance from the apex and later decreased with senescence. North (1958a) stated that P/R ratios varied considerably with the type and age of the tissue. McFarland and Prescott (1959) reported a P/R ratio of 1.8 for the kelp at a depth of three meters.

Clendenning and Sargent (1957) found that photosynthesis was sharply depressed when calcium was reduced, and stopped in one hour when calcium was omitted completely. They also reported that photosynthesis was not limited under heavy bryozoan encrustation under saturating light intensity, but that the encrustation did mechanical damage to the plant (plants became brittle, and often sank under the weight). Clendenning and Sargent (1957) calculated that under heavy encrustation by Membranipora, respiration by the bryozoan on one blade surface was equal to that of the blade, but that the green algae in

the animal colonies raised the net and total photosynthetic capacity of the encrusted kelp complex about 50% above that of the kelp itself. At 2500 f.c. photosynthesis in the green algae exceeded respiration in the bryozoan. It would appear that light intensity of this magnitude would only prevail at the surface. They also found that the compensating light intensity for the encrusted kelp was 100 f.c. as compared with 30 f.c. for clean kelp.

Sargent and Lantrip (1952) calculated rates of photosynthesis, rates of increase of organic matter/day and rates of export of organic matter/day for blades from the apex to the bottom of giant kelp fronds. They found that blades at the apex of a frond increased faster than would be provided by their photosynthetic product, and that in summer the daily rate of organic matter production by a frond exceeded the rate of growth. They inferred massive translocation of organic matter through the stipe. Parker (1963), using C^{14} - labeled bicarbonate, demonstrated that organic products were transported through the stipe, the direction being either predominantly apical or toward the base.

McFarland and Prescott (1959) reported Chlorophyll a values for the giant kelp (Tables 2,3). They also stated that kelp respiration (13-15 g O_2/m^2/day) and gross photosynthesis (13-16 g O_2/m^2/day) were indicative of a high production (Fig. 10). Using assimilation numbers (g O_2/g Chl./hr) they concluded that the giant kelp system had a productive capacity similar in magnitude to that of coral reefs, springs, and marine grass flats.

Principal Food Chains

A great variety of life has been reported from the giant kelp beds. Quast (1960b) stated that kelp beds created additional sources of food for fishes. The erect plants increased the surface area for invertebrate attachment, normally present only on the bottom. Encrusting animals such as bryozoans act as additional substrates for crustaceans such as ghost shrimps. Dawson et al. (1960) listed 114 algal species associated with giant kelp beds.

It would appear that two principal food chains are associated with kelp: the grazing and the detritus chains. Within each type are sub-categories which induce a complexity of energy transfer.

Leighton et al. (1966) observed that grazing was always present in giant kelp beds. They reported that fishes, crustaceans, gastropods, and echinoids usually comprise the majority of macroscopic grazers on giant kelp. Undoubtedly, the predominant grazers on giant kelp, from the standpoint of destruction are echinoids, principally Strongylocentrotus purpuratus and S. franciscanus. They particularly concentrate on sporophylls, later attacking the primary stipe which results in frond loss after the sporophylls are consumed. Leighton (1960c) observed these urchins moving as a front through stands of algae and removing all plants.

The balance between plant production and grazing can be offset as different temperatures have unequal effects on the rates (Leighton et al., 1966). The Q_{10} for kelp photosynthesis is 2.0 (Clendenning, 1958c) and that for frond elongation is 1.7 (North, 1965b) Leighton (1960a) found that the rate of kelp consumption for S. purpuratus over the range 5 - 15°C., expressed as percent of body weight, was almost quadrupled. Above 17°C. consumption rate declined. Thus, in the optimum temperature range for kelp growth, urchin consumption was twice

TABLE 2
MEAN CHLOROPHYLL "A" CONTENT OF THE VARIOUS PARTS OF MACROCYSTIS PYRIFERA IN MG . CHLOROPHYLL/GM. OF WET TISSUE. (AFTER McFARLAND AND PRESCOTT, 1959).

	Locality					
	Paradise Cove, June 1959			Santa Catalina, December 1958		
Plant Part	Mean Chl. mg./gm.	Range	No. Samples	Mean Chl. mg./gm.	Range	No. Samples
Holdfast	0.026	0.019-0.035	8	0.017	0.008-0.031	5
Stipes	0.043	0.021-0.063	12	0.022	0.014-0.033	6
Bulbs	0.039	0.027-0.054	10	0.012	.....	1
Blades	0.207	0.163-0.278	10	0.218	0.187-0.256	7
Fruiting Blades	0.234	0.128-0.310	6	.....	.....	...

TABLE 3
CHLOROPHYLL "A" DISTRIBUTION IN VARIOUS PARTS OF THE GIANT KELP, MACROCYSTIS PYRIFERA (AFTER McFARLAND AND PRESCOTT, 1959).

	Chlorophyll "A" in each component in per cent of total chl./m^2 bottom					
Depth of Water in Meters	Holdfast	Stipes	Bulbs	Blades	Fruiting Blades	Total for Entire Plant in gm. chl./m^2 of bottom
6	1.92	4.18	3.86	84.79	5.26	0.62
9	1.81	6.49	3.91	83.13	4.66	0.78
12	5.77	8.50	6.05	77.88	1.80	0.57
Average Value	2.99	6.34	4.51	82.15	4.02	0.66

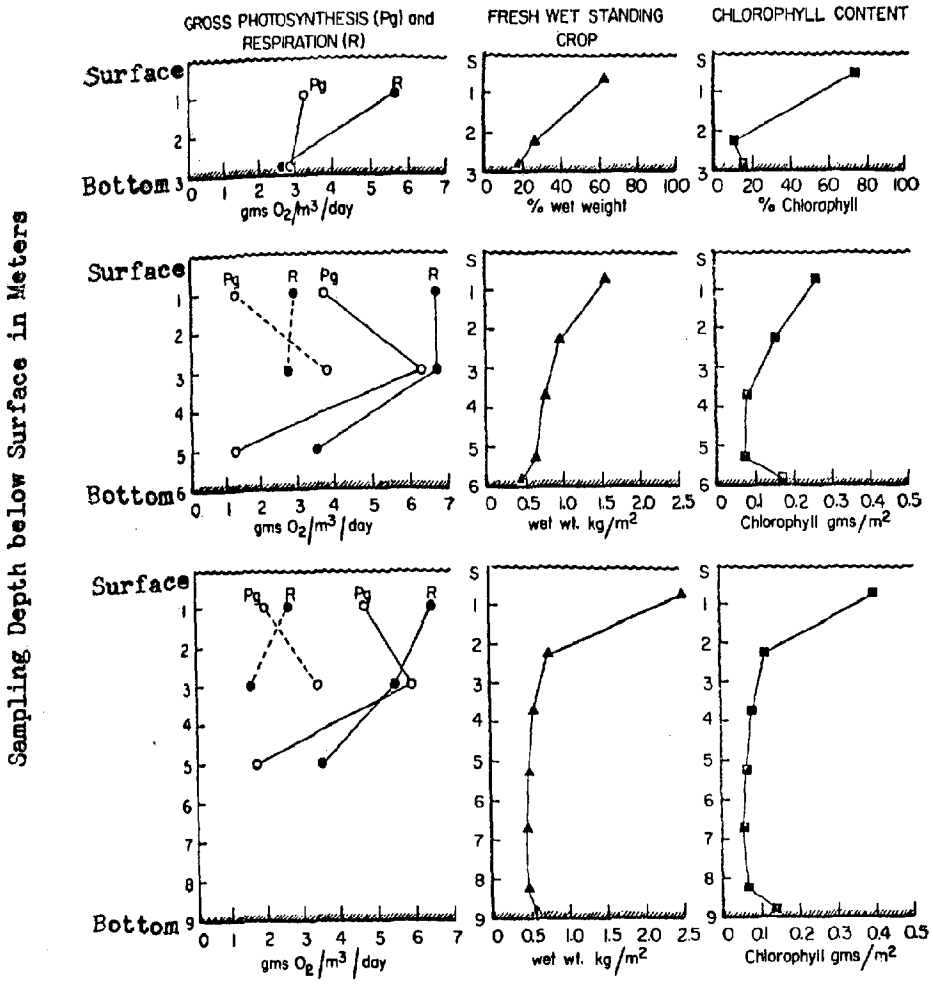

Fig. 10. Gross photosynthesis (P_g), respiration , vertical distribution of wet biomass and vertical distribution of chlorophyll 'A' for the Paradise Cove kelp bed in 3, 6, and 9 meters depth. The dark lines for the P_g and R graphs represent the total metabolism including plankton. The dotted lines represent the total P_g and R for the kelp community minus the planktonic P_g and R. The values for P_g and to a lesser extent R for the surface water are underestimated. (After McFarland and Prescott, 1959).

the production rate of giant kelp. Thus, urchins can denude an area of all algal growth and keep it barren, unless supplied with an outside source of food. This occurs when sewage enters an area. Urchins participate in both types of chains, and in the absence of their preferred role as grazers, can utilize detritus for survival. The difficulty arises when kelp beds diminish, as they do during warm water periods; the urchins consume kelp faster than the plants produce new growth. The kelp area can become barren. Then, the urchins transfer to the detritus chain for leptopel. They are thus adaptable to a varying source of food and can keep an area barren that has once become imbalanced.

Leighton et al. (1966) stated that a fish, the sheephead (Pimelometopon pulchrum); the sea otter (Enhydra lutris); and two asteroids, the sunstar Pycnopodia helianthoides) and the sea star (Astrometris sertulifera) are natural predators on urchins in southern California. Of these the otter is the only effective controlling agent, preying vigorously on predominantly S. franciscanus. Otters formerly were numerous south in Baja California, but hunters reduced them, and they came close to extinction. Leighton et al. (1966) stated that their number presently ranged between 400 - 600. North (1965b) reported that by 1964 urchins became extremely scarce in southern Monterey Bay, presumably due to otters. Before 1963 urchins were dense. Extensive beds of kelp and other seaweeds appeared by 1964. McLean (1962) reported that Dr. Boolootian observed 50 otters eating 5280 S. franciscanus, 301 Mytilus californianus (a detritus feeder), and 380 Haliotis rufescens (red abalone, also a giant kelp grazer). Thus under protection the sea otter should provide the balance necessary between urchin predation and kelp growth.

Among the other grazers on kelp are gastropods. The best known one is Haliotis rufescens, red abalone. Leighton (1960b) reported that the holdfast of giant kelp supported a large number of young abalone, but was not requisite for survival. He stated that in the field both young and adult forms grazed on sporophylls in the area of the primary stipe.

Leighton (1966) studied food preferences of 11 invertebrate grazers in giant kelp beds: three enchinoids (urchins), six gastropods (three were abalones), and two crustacea. The animals were common to giant kelp beds; all plants used represented the major floral elements of the kelp community. All grazers exhibited high degrees of preference for giant kelp (Table 4).

Wing and Clendenning (1960) found that a number of crustaceans grazed preferentially near the pneumatocyst which ultimately resulted in healthy blades being sloughed off. Two were isopods, Paracereis sp. and Idothea resecata, the kelp isopod. The latter animal is consumed by the kelp bass. Three other crustaceans were nest-forming gammarid amphipods, Ampithoe, Hyale frequens, and an unidentified species. He stated that gammarids were voracious grazers and were one of the main causes of tracks and burrows in the blades and pneumatocysts. They were also regularly found in fish stomachs.

The blades and holdfasts of giant kelp harbor a large number of invertebrates. Limbaugh (1955) listed 25 species found associated with the canopy and many more in the holdfasts. Menzies (1957) described several species of Limnoria, a boring isopod, on holdfasts and the basal ends of stipes. Their burrows were often inhabited by other crustaceans and polychaete worms. Andrews (1945) observed 640 - 1300 invertebrates/m^2 of holdfast in Macrocystis integrifolia. They used the holdfast for food and protection. These animals were scavengers and carnivores, mostly in the larval or juvenile stages. They included snails, crabs, shrimp,

TABLE 4

SYNOPSIS OF PREFERENCE ORDER RANKINGS OF ELEVEN HERBIVORE SPECIES ON ALGAE. (AFTER LEIGHTON, 1966).

GRAZING SPECIES	*Macrocystis*	*Egregia*	*Laminaria*	*Eisenia*	*Pterygophora*	*Cystoseira*	*Gigartina*
Aplysia	2	1	6	4	5	7	3
Astraea	1	3	4	5	7	6	2
H. corrugata	1	2	4	3	5	6	7
H. fulgens	2	1	3	4	6	7	5
H. rufescens	1	2	3	4	6	7	5
Lytechinus	2	4	3	5	7	6	1
Norrisia	3	1	2	5	4	7	6
Pugettia	1	2	4	6	3	5	7
S. franciscanus	1	6	3	4	5	7	2
S. purpuratus	1	4	2	5	6	7	3
Taliepus	1	2	3	5	4	6	7
Total (W_t* = 0.61)	16	28	37	50	58	71	48

* W_t = Coefficient of concordance for mean preference orders of all grazing species (see text); the value is significant at better than the 0.1% level.

isopods, worms, chitons, amphipods, brittle stars, bivalves, anemones, starfish, urchins, cucumbers, and tunicates. Many of these consumed holdfast material, weakening the holdfast, resulting in loss of whole plants during autumn and winter storms (Andrews, 1945). Ghelardi (1960) wrote a major paper on animal communities in giant kelp holdfasts.

Wing and Clendenning (1959) reported populations of motile invertebrates, up to 100,000/m^2, on blade surfaces heavily encrusted with Membranipora or attached hydroids. This density was 25 - 28 times the numbers of motile animals on clean blades. It is probable that the animals accumulate on the blades for shelter and use them as a base for gleaning food from a flowing current. Animals which associate with kelp blades include ostracods, copepods, amphipods, decapods, polychaetes, nematodes, turbellaria, and molluscs. Most, if not all, of these are consumed by fishes.

Owing to the interest in sports fishing much work has been done on the fishes associated with giant kelp beds. Some fish are grazers on the kelp; others are carnivorous and eat grazer intermediates in the kelp food chain.

Davies (1968) listed the 25 main species of fish caught in the giant kelp beds or in the immediate vicinity. Of the first 14, nine were pelagic species. He added that the presence of giant kelp was not essential for the spawning of any of the main species caught in the sportfishery, but that the beds do provide shelter, refuge, and food for larval, juvenile, and even adult stages for many fish. He emphasized that giant kelp provides a habitat of sufficient complexity so that a multitude and variety of organisms could be supported. Limbaugh (1955) recorded 125 species of fish from the kelp beds, but the majority were also found in areas without giant kelp.

Quast (1968c) listed 44 fish species attributed to the kelp and rock habitats from three quantitative collections. He found that kelp bass, California sheephead, and blacksmith were the most frequently encountered species in kelp beds of the San Diego region. Quast (1968b) reported average densities for these three fishes from kelp beds: a. Kelp bass - 20/acre, b. Sheephead - 14/acre, c. Blacksmith - 448/acre. Giant kelp was not a prerequisite for the latter species.

Quast (1968b) listed standing crops of resident kelp bed fishes from three areas: a. Bathtub Rock where kelp was moderately dense but short with no canopy - 296 pounds/acre; b. Papalote Bay where kelp was dense but long with a considerable canopy--307 pounds/acre; c. Del Mar with a kelp bed close to upwelling water --335 pounds/acre (Table 5). These values would be increased by inclusion of invertebrates such as the lobster, abalone, and octopus, and nekton such as sharks and barracuda, all forms often sought by sport fishermen. These standing crop values were close to median values from lakes and coral reefs.

Quast (1958, 1968d) made a thorough analysis of food habits of 15 and 45 kelp bed fishes, respectively. Davies (1958) stated that the kelp bass was the most important fish caught in or near kelp beds. Quast (1960a) found that four fish species grazed on kelp, the opaleye, halfmoon, senorita, and the zebraperch. The first two are desirable for the sportsfisherman. Quast (1968d) reported that the barracuda ate the senorita. I do not have specific data to substantiate this statement, but I would guess that barracuda and sharks are omnivorous in feeding on fish species. Other species such as kelp rockfish and sheephead are

TABLE 5

CORRECTED STANDING CROP ESTIMATES FOR FISHES

Based on the three quantitative collections with substitution of transect values for kelp bass, sheephead, and opaleye. Applies principally to beds 25-35 feet in depth. (After Quast, 1968b).

	Pounds per acre		
	Del Mar	Bathtub Rock	Papalote Bay
Transect-based estimates			
Kelp bass[1]	105	105	105
Sheephead[2]	43	43	43
Opaleye[3]	72	72	72
Total	220	220	220
Quantitative collections			
Other fish species	115	391 (76)[4]	87
Total	335	611 (296)[4]	307
Average (excluding barracuda) = 313 lbs. per acre			

[1] Based on average weight of 2.1 lbs. and av. density of 50 per acre (see text and Table 15).
[2] Based on average weight of 2.5 lbs. and av. density of 17 per acre (see text and Table 17).
[3] Based on average weight of 1.8 lbs. and av. density of 40 per acre (see text and Table 23).
[4] Value in parens. excludes barracuda.

desirable, but assessment cannot be made here of all species fished for.

Young kelp bass contained amphipods, spider crabs, pistol shrimp, and isopods. Larger forms contained fishes and cephalopods.

The opaleye contained algae, including giant kelp. Quast (1968d) reported that young forms contained a 50:50 ratio of plants and animals, but that adults contained a predominance of plants.

The halfmoon contained a variety of algae, but with giant kelp being a principal source of the plant food. Bryozoans and sponges were also found.

The senorita appears to be omnivorous, with principal foods being small gastropods and crustaceans associated with algae (opossum shrimp, amphipods, shrimp, copepods, ostracods, bryozoan larvae). Numerous giant kelp fragments have been observed.

The contents of zebraperch were similar to those of opaleye and halfmoon, but the conclusion was that the algae was consumed along with the grazing for animals.

Much attention has concentrated thus far on the grazing chains. This obviously related to the conspicuous forms which constitute them. The detritus chains are nourished by algal breakdown, in large part from giant kelp plants set free by biological and physical agencies, by particulate matter from sewage, or by bacterial ingestion. Urchins and starfish can subsist on detritus, as can a variety of other animal forms. This list may include brittle-stars, sea cucumbers, clams, anemones, bryozoans, hydroids, many crustacea, a multitude of worms, and nematodes. Many of the detritus feeders are intermediates in the grazing food chains of the commercially valuable fishes.

Fig. 11 diagrams some of the principal food chains with a few of the more obvious forms.

A report by the California State Water Quality Control Board (1964) gives an excellent account of invertebrate grazers on giant kelp.

KELP SYSTEMS AND MAN

Involvement With Economic System

The giant kelp system is of great economic benefit in at least two ways: the plants themselves are harvested and processed for their chemical content and for use as food additives or fertilizer, and many of the animals such as fish, lobsters, and abalone are collected for food and for recreation (North, 1959).

Scofield (1959) stated that in California three or four kelps were commerically important, but that giant kelp was the one most harvested from 1910 until 1959. He gave an exhaustive historical account of kelp use in California. He indicated that two companies were foremost in kelp harvesting and use at the present time, the Philip R. Park Inc., San Pedro, and Kelco Company, San Diego. North (in press) added a third, the Kelp Organic Products Co., Los Angeles, which markets dried kelp for fertilizers.

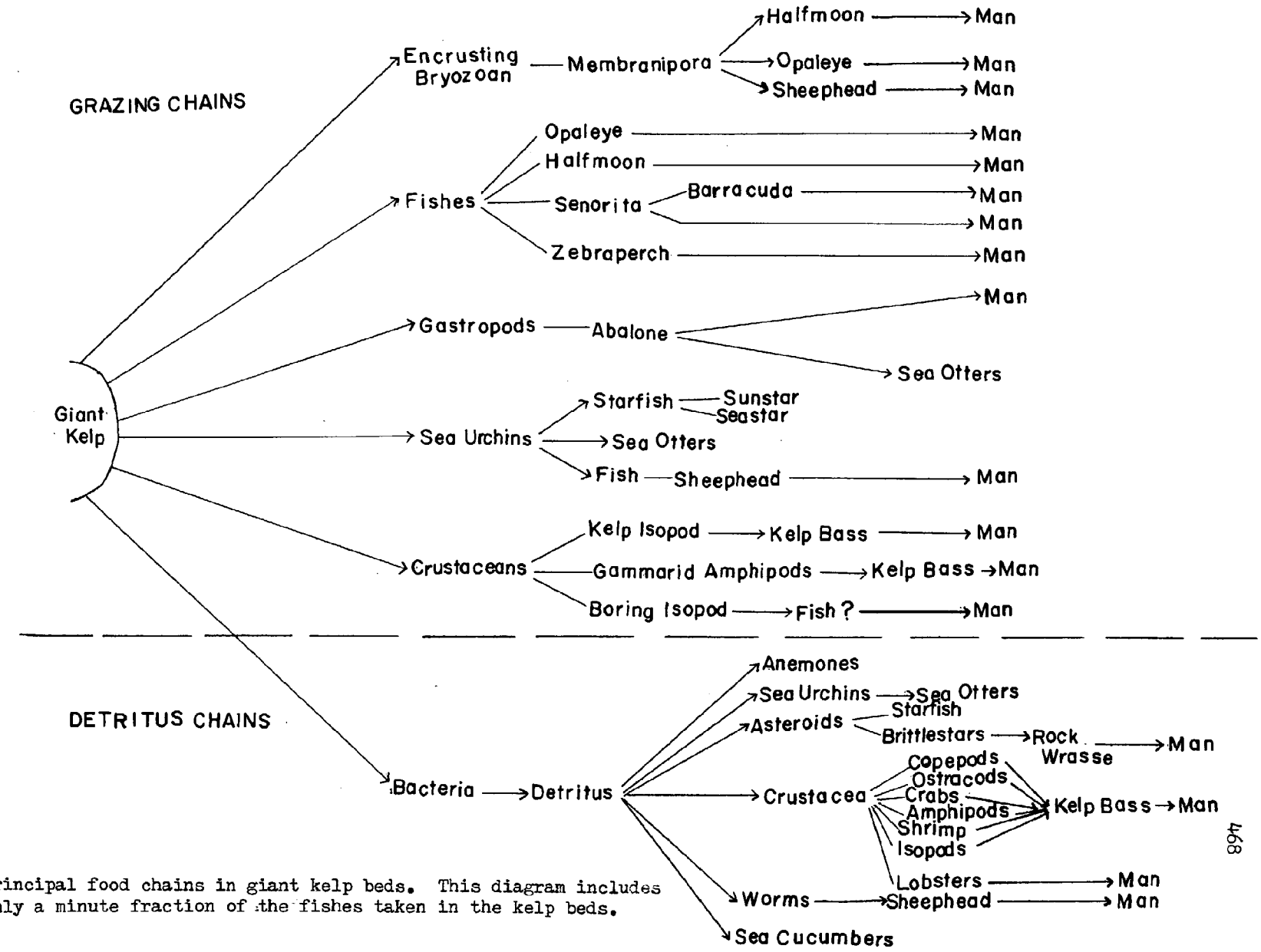

Fig. 11. Principal food chains in giant kelp beds. This diagram includes only a minute fraction of the fishes taken in the kelp beds.

Income for kelp harvest is of benefit not only to the industry, but also to the State of California. North (1960c) estimated giant kelp coverage in southern California at slightly more than 100 square miles, but North (1968c) found this coverage to be reduced to one-half to three-fourths as large. Scofield (1959) stated that in 1950 the State of California, in cooperation with the industry raised annual leasing fees to $100.00/square mile plus a state tax on kelp to $.10/wet ton. Mr. K. F. Gibsen, Kelco Company, related that the state tax varied from $.10 to $.50, with the average value being close to the minimum figure (personal communication). North (1964b) estimated that the annual harvest ranged between 100,000 - 150,000 tons of wet weight kelp. A very conservative estimate gives an annual state income of $15,000.00 which Scofield (1959) stated was used to aid administrative costs and research by the California Fish and Game Commission on the giant kelp system. It can only be said that basic biological research on giant kelp in California has been exemplary.

North (1964b) found that the kelp harvested annually had a commercial value of $20.00/wet ton. With the annual harvest listed at 100,000 - 150,000 tons, this places the annual landed value of giant kelp at about two million dollars. North (1968c) reported that dried kelp sells for $90.00 - $125.00/ton. He added that the major portion of the California harvest is processed for algin, with prices varying from $.05 - more than $1.00/pound, depending on the quality or grade. In 1941 the production of algin in the United States was worth approximately $1,500,000.00. Most of this came from California.

North (in press) has published an exhaustive review of the value of giant kelp to the industry and for sportsfishing. Since the manuscript has not been formally published at the time of this writing, I do not feel the liberty of using the data. Perhaps a summary statement of the total worth of the system could be made. He reported that taken together the kelp harvesting and commercial fishing industries probably gather two to four million dollars/year of natural resources from the California kelp beds as landed values. Conversion to market values increases the worth about fourfold. If all use of the beds by owners of private boats, partyboats, and the savings derived from marine waste disposal was considered, the total value of the giant kelp system could be reckoned in tens of millions of dollars (North, in press). This reference will be an extremely valuable one for an exhaustive treatment of the giant kelp system.

Giant kelp is used by industry in a variety of ways. Scofield (1959) gave a complete historical review of the use of giant kelp. Former uses have been for potash and acetone for ammunition. Iodine was once extracted. Both these uses have been discontinued. North (1968c) stated that almost all the California kelp harvest was for alginic acid, a complex polysaccharide. An analysis of fresh giant kelp gave a water content of 82%, algin content of 2.2%, crude fiber content about 1%, and a nitrogen content about 0.2% (North, 1959). Chapman (1952), reporting on data in a paper by Hoagland, listed an algin content variation of 1.8 - 2.7%, depending on locality and portion of the plant sampled. Content of blades was higher than that of stipes. Vaughan (1959) stated that alginic acid comprised about 20% of giant kelp, dry weight. He listed the major components of giant kelp (Table 6). The book by Chapman (1952) was an exhaustive treatment of the uses of algae up to publication date.

TABLE 6

MAJOR COMPONENTS OF M. PYRIFERA. (AFTER VAUGHAN, 1959).

The per cent composition for the major components of Macrocystis pyrifera was estimated after the components had been partially separated by extractions with 80% ethanol, ether, 20% KOH in ethanol, 0.5 M HCl, and 2% Na_2CO_3.

Component	Method of Estimation	Approx. per cent
Moisture	Difference between oven-dried sample at 102° and the sum of the fractionated components dried over P_2O_5 for several weeks	10.3
Total ash	Weight of dry ash	40.0
Ether solubles		1.4
Mannitol	Crystals + dissolved mannitol in ethanol supernatant	14.8
Laminarin	Glucose in hydrolysate of water extract	0.3
Fucoidin	Total water-soluble polysaccharide less laminarin	2.1
Alginic acid	Weight of purified sample	19.0
Cellulose	Residue after extractions	0.5

Owing to the colloidal nature of algin, it can absorb large quantities of water. It is used to stabilize a large variety of products where materials are required to remain in suspension. A publication of the Kelco Company, called Kelp, states that there are over 100 algin applications

Documented Disturbances and Demonstrated Effects

North and Clendenning investigated the effects of sewage and oil on giant kelp photosynthesis. Most of these are laboratory analyses and will be summarized. There is one good documented case history of oil pollution in the field (See Chapter E-11).

On 29 Marsh 1957 the tanker ship Tampico, carrying 59,000 barrels of diesel fuel oil struck a rocky point about 50 miles south of Ensenada, Baja California, liberating a large amount of oil. The half-sunken ship blocked off half the entrance to a small cove. Area of the shoreward water was about 10,000 square yards, and its depth did not exceed 20 feet. The area was first visited by North on 25 April 1957. The area supported a typical giant kelp system. On 10 June and 10 July 1957 North observed a large number of young kelp plants, the largest being about 50 cm. in height. Overall effects of the accident were widespread. Large quantities of fish, clams, mussels, lobsters, abalones, echinoderms, and other animals were killed outright and washed up on the beach. Some intertidal algae seemed to be damaged by the oil scum at the surface, but diving observations revealed an extensive growth of benthic algae close to the wreck. Several healthy adult kelp plants were found close to the wreck, one very large plant as close as 50 feet on the leeward side. The evidence indicated that the young kelp plants had settled in the area just before and shortly after the accident. All evidence indicated that the oil eliminated the grazers, suggesting strongly that grazers, particularly the urchins, were a controlling factor in the establishment of the kelp bed. North revisited the area in July 1958, after storms had torn apart the wreck in winter 1957-1958. With the wreck intact, plants were protected from wave shock. In May 1958 a considerable decrease in kelp concentration was noticed, but in July 1958 a heavy canopy had developed. Animals were again becoming common in the area of the wreck, mostly a few fish and an abundance of shore crabs, Pachygrapsis (North, 1957, 1958b; Neushul, 1958).

Clendenning (1959a) stated that North collected a water sample heavily contaminated with oil from a tidepool at the Tampico wreck site. After standing for weeks, four stable zones were evident: a voluminous bottom sludge, relatively clear water occupying about 2/3 of the sample volume, a voluminous top sludge, and a surface oil film. When the sample was shaken the clear water zone contained tiny oil globules, and the water appeared turbid. Tests demonstrated that oil emulsification could occur in surf. This evidence was used to explain the spread of oil released by the Tampico to benthic animals to the 20 foot depth.

Clendenning (1959a) subjected kelp blades to varying concentrations of diesel fuel oil and boiler fuel for varying lengths of time. Figs. 12, 13 and 14 reproduce some of his data on the effects of oil on photosynthesis (Clendenning, 1959b).

Clendenning (1959a) reported that more than one day was required for measurable injury to kelp blades during severe oil treatments. He added that after 24 hours' exposure, all blades demonstrated high photosynthetic capacities.

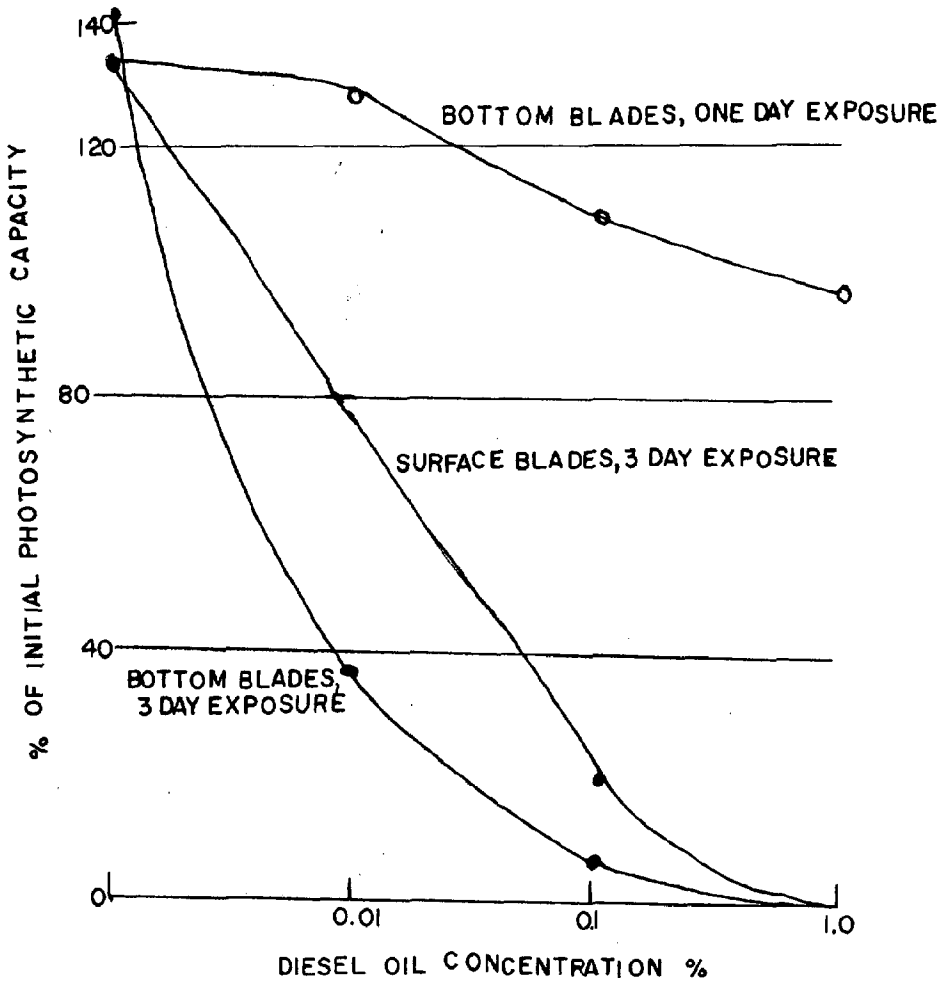

Fig. 12. Inactivation of kelp photosynthesis during continuous exposures to diesel oil-sea water emulsions. (After Clendenning, 1959b).

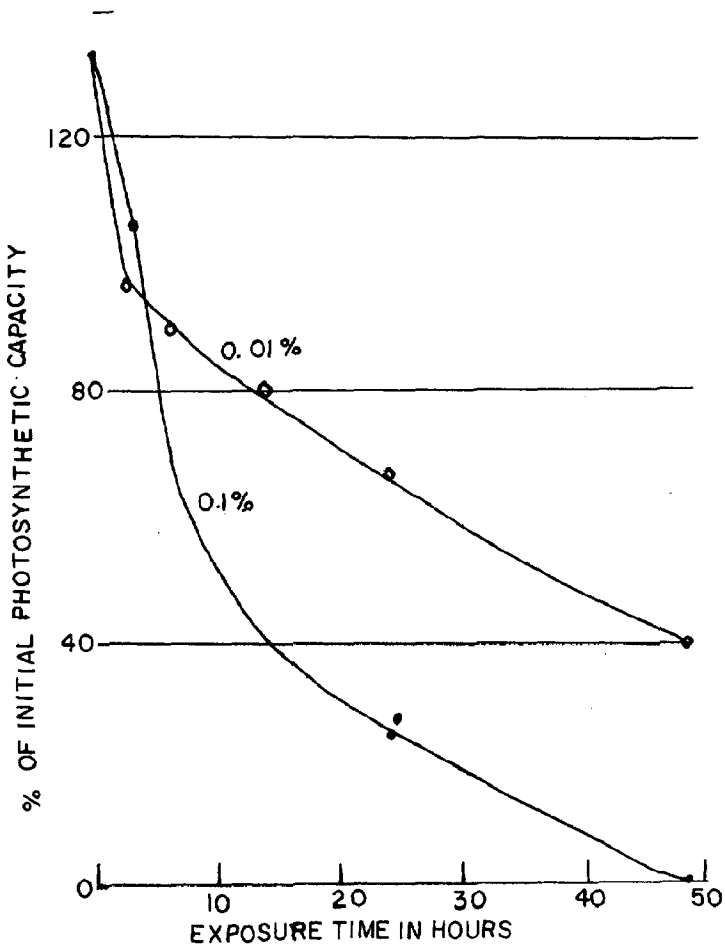

Fig. 13. Inactivation of photosynthesis in half-grown bottom kelp blades following brief exposures to Tampico diesel oil-sea water emulsions. (After Clendenning, 1959b).

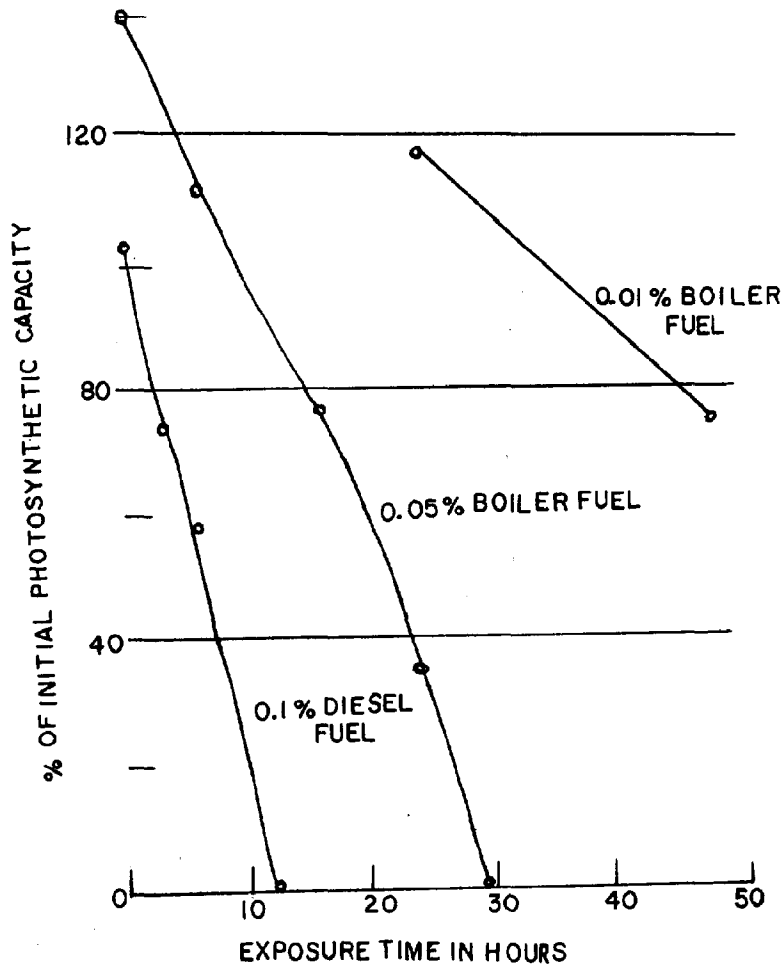

Fig. 14. Inactivation of photosynthesis in half-grown bottom kelp blades following brief exposure to Navy diesel and boiler fuel emulsions. (After Clendenning, 1959b).

This seems to conflict with his data in Figs. 13 and 14, which may suggest that oil toxicity may depend on a set of factors in the field, i.e., chemical activity of the seawater, water turbulence which would control oil concentration in the water, and possibly the way oil influences water turbidity which may by itself weaken the plant by slowing photosynthetic capacity. Clendenning (1959a) concluded that kelp fronds could be exposed to emulsified diesel oil for only six to 12 hours without irreversible damage. A lag phase was also noted in which visible injury due to oil did not become apparent for about two days. He stated that black boiler fuel had a strikingly greater toxicity on kelp than diesel fuel. It is probable that the survival and gain of giant kelp in the field following the Tampico wreck was due to a dilution of oil beyond the toxicity level or that the bottom and top sludges were not emulsified into the clear water layer by turbulent water. It is also clear that oil residues are persistent and long-lasting, and the potential of their effects measured in time can be great. Tampico water samples retained emulsified oil in sludge fractions for two and one-half years.

As to metropolitan and residential sewage, the relationship to kelp growth is inconclusive. North (1964b) noted that in the past two decades an extensive thinning or complete disappearance of kelp beds occurred near Los Angeles and San Diego. These losses were based on area measurements and harvest returns. They came at a time when sewage flow rates were increasing.

A variety of sewage constituents are produced. North (1960c) reported that industrial wastes pouring into Los Angeles Harbor included effluent from fish canneries, oil industries, vegetable oil plants, creosoting and pile treating, metal working shops, and shipbuilding and repair shops. Domestic wastes came from private sewage disposals, ships and boats, and from metropolitan treatment plants. The effluent comprised both liquid wastes and suspended solids.

Leighton et al. (1966) stated that an ecological imbalance, resulting in significant destructive grazing, could arise from two causes: inimical conditions could reduce productivity to a level where it cannot sustain grazer demands, and consumption requirements could increase. Data showing inordinate consumption increase rates of urchins over photosynthesis in giant kelp has already been presented. It is obvious that waste discharges in or near kelp beds has created an ecological imbalance (Leighton et al, 1966). Both North (1964b) and Leighton et al. (1966) reported that kelp decreased near the metropolitan discharges of San Diego and Los Angeles. North (1960c) found bed decreases near the Santa Barbara outfall.

The big problem was to determine the precise effect of sewage on the plants. Several possibilities were offered: toxicity of sewage (North, 1957), creation of favorable environments for kelp grazers (North, 1957, 1964b), sedimentation which might render the substrate unfit for development of kelp spores, the reduction of water clarity which might reduce growth below grazer consumption levels, and the increase of the BOD (North, 1964b).

Clendenning (1958a) studied the effects on kelp of three elements normally present in sewage, i.e., copper, chromium, and chlorine (Fig. 15). Reduction in photosynthetic capacity was used as the index of toxicity as the data could

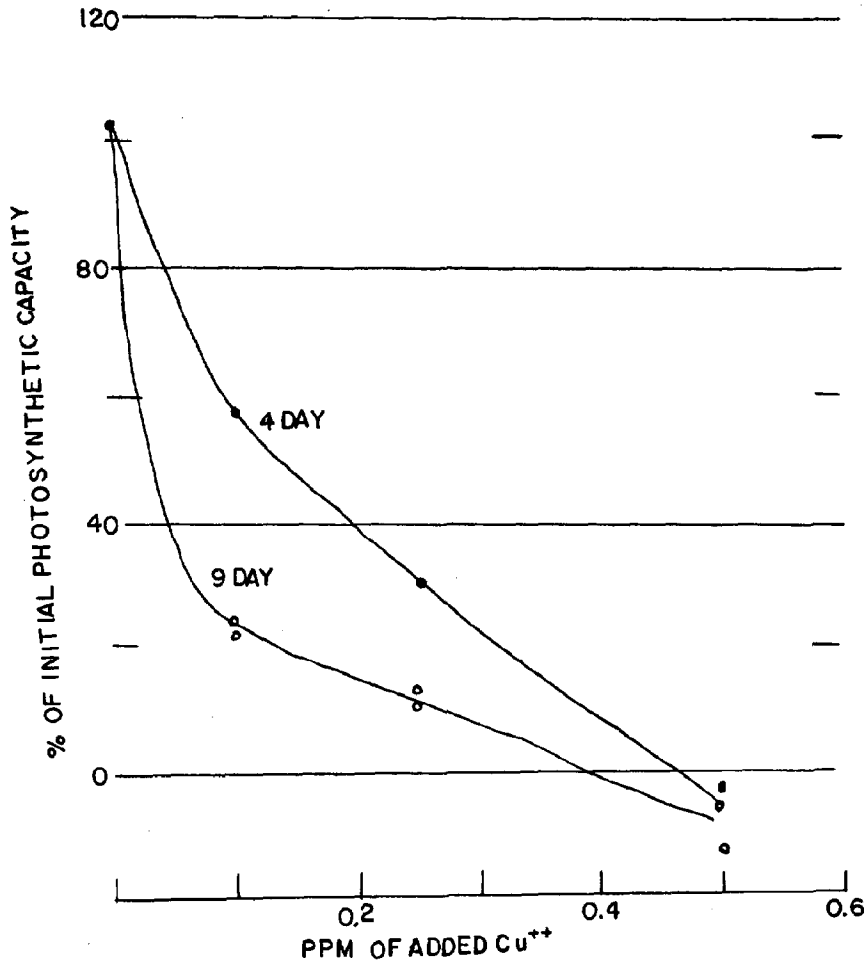

Fig. 15. Inactivation of photosynthesis in half-grown kelp blades following 4-day and 9-day exposures to 0.1 - 0.5 ppm Cu^{++} in sea water at 15°C. (After Clendenning, 1959b).

be quantified and changes appeared before visible symptoms of injury. The lowest copper concentration which was toxic to giant kelp was 0.1 ppm (threshold between 0.01 - 0.1 ppm). Chromate was strongly toxic to young blades at 10 ppm, but only slightly at 1.0 ppm, and not at all at 0.1 ppm. He stated that net photosynthesis was eliminated and blades were visibly damaged by two days' exposure to 10% unchlorinated sewage. Using 10% chlorinated sewage there was 20% retention of photosynthesis, but after two days' exposure blades deteriorated rapidly. When sewage was diluted 100-fold, no toxic effects were observed in either unchlorinated or chlorinated effluent. Clendenning (1959a) demonstrated that kelp blades in 10^{-4} M or 94 ppm of phenol displayed no effect, but that blades in the presence of 10^{-3} M phenol displayed a photosynthetic capacity reduction of 30%. All blades exposed to phenol displayed higher respiration rates than controls. Blades placed in solutions of chlorinated phenols with concentrations of 10 ppm either strongly reduced or eliminated photosynthesis.

Clendenning (1960a) studied the effects on kelp of Los Angeles waste waters from four sources. Domestic sewage had no adverse effect on kelp in the dilution ranges of 50-fold, 100-fold, and 200-fold. Photosynthetic capacities even seemed to be slightly stimulated by the 50-fold dilution. Oil refinery wastes were strongly toxic to kelp after a 50-fold dilution (50% reduction in photosynthetic capacity in four days' exposure), but had no detectable effect when diluted 200-fold. Oil field brines completely eliminated photosynthesis after four days in young blades, and up to 80% in mature blades (1 - 2% concentrations) (Clendenning, 1960b). The toxicity of toluene, benzene, and n-hexane was determined at 10 ppm in seawater. Toluene was the most toxic of the three compounds. After four days photosynthetic capacity was reduced as much as 80%, accompanied by visible injury to blades. Blade response to benzene was small and less to n-hexane. Photosynthesis was eliminated by two days' exposure to 2 ppm detergent (sodium tetrapropylene benzene sulfonate), but was unaffected by a concentration of 0.5 ppm.

Despite all these data several references concluded that reductions observed in kelp beds resulted from factors other than discharged wastes. North (1964b) noted that healthy kelp persisted in areas with heavy waste discharge. He added that the toxicity thresholds of heavy metal ions and organic substances was not sufficiently harmful in the concentrations ordinarily found in effluents to have caused the extensive losses observed. Studies of the beds as they were disappearing did not reveal any direct damage which could be attributed to wastes from metropolitan outfalls. He added that the losses were always traceable to natural causes which occurred frequently in other beds away from discharged wastes. On the other hand he allowed for an ecological imbalance, as the typical processes of succession were not in evidence. Other references on this point are North (1960b, 1960c) and Clendenning (1958b).

Large scale fluctuations and disappearances are not uncommon in beds far removed from discharged wastes, but sooner or later reestablishment occurs. There seems to be a firm basis for suspecting that an adverse influence has been exerted on the kelp at Palos Verdes and Point Loma by discharged wastes. Any explanation of this must account for the persistence of kelp to 1000 feet or less of the Santa Barbara outfall. Of the possible adverse mechanisms (toxicity, sedimentation, disease) none seemed to be as likely as benthic grazing, possibly

complicated by changes in water clarity (California State Water Quality Control Board, 1964).

Leighton et al. (1966) found indications that sewage could encourage urchins and thereby change the ecological balance between seaweeds and grazers. They calculated that organic matter supplied by sewage (380 g. organic matter/m^2/year) could maintain urchin stocks whose requirement (126 - 375 g. organic matter/m^2/year) exceeded that which kelp could supply (78 mg. - 36 g. organic matter/m^2/year). Leighton (1960a) observed urchins completely denuding an area of all plants.

Zobell (1946) reported that bacteria could oxidize and assimilate hydrocarbons. Thus, Clendenning (1959a) theorized that oxygen deficits could develop under oil pollution, and that these deficits could be toxic to kelp. He then stated that no evidence indicated that oxygen deficit was involved.

Other factors have been observed to harm giant kelp growth and vigor. Warm and turbulent water are inimical to growth. Water clarity, which may be reduced by turbulence, but also by sewage and oil pollution, is an important consideration from the aspect of growth and vigor. North (1960c) stated that the adult plant is normally fairly immune to changes in water clarity because of the canopy, but the canopy could be damaged by warm water. North (1967b) stated that the canopy absorbed from 80 - 90% of the light entering the water. Thus, future plant growth from below could be jeopardized by high turbidity levels. North (1960c) also stated that discharged liquid wastes possess very high light absorbing capacities. Part of the problem comes from the possible nourishment of plankton growth in the water mass by waste discharges, which could then increase the overall turbidity, as well as selectively filter out those portions of the visible spectrum which support kelp growth (North, 1960b). Thus, the effects of sewage disposal on giant kelp in the field seem to be mainly indirect.

Some data on light penetration were given in the section on Vertical Patterns. Clendenning and Sargent (1958) indicated that near the bottom in deep water, insufficient light penetrated to allow for growth. Thus, new growth on older plants derives energy by translocation from mature fronds. Light response is complicated by factors such as non-linear response of photosynthesis to increasing light intensity (Fig. 16), variation of photosynthetic capacity with age of tissue and with temperature, dependence of photosynthesis upon spectral quality of light (Fig. 7), uneven spectral absorbance and scattering within the water column (Fig. 17, 18), etc.

North (1958a) indicated that an increase of 1% in absorption coefficient could result in a 20% loss in net photosynthesis at a depth of 15 meters (Fig. 19). Fig. 8 listed the theoretical photosynthesis at different depths of blades with an indication of the compensation point in waters of different absorbancies. It thus appears that slight changes in water clarity which result from normal factors and reinforced by waste discharges can have far-reaching effects on giant kelp.

North (1967b) reported that increasing water absorbance reduced total photosynthetic capacity (Fig. 20). The effect was more pronounced in plants with smaller canopies. He concluded that the development of a massive canopy conferred a great advantage in very turbid water. Fig. 21 diagrams the depth effect

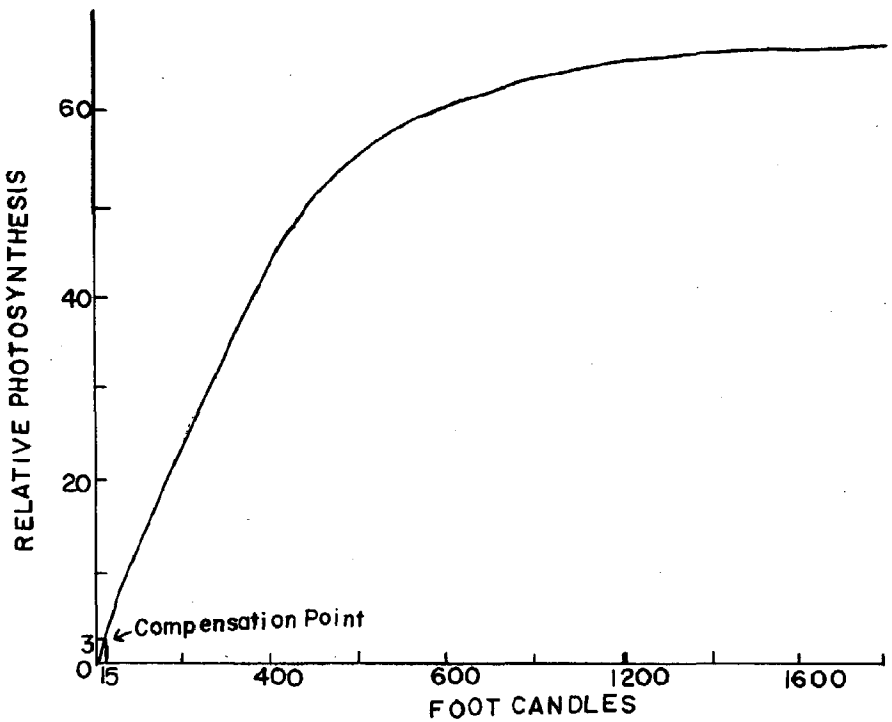

Fig. 16. Graph illustrating the changes in photosynthetic rate in adult Macrocystis blades as a function of light intensity. P/R ratio of 22 assumed (After Clendenning and Sargent, 1957).

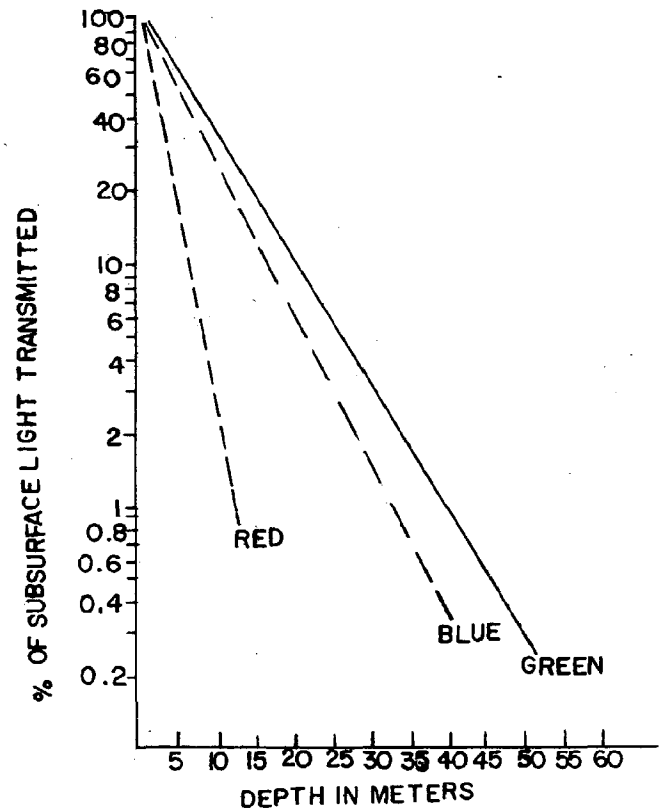

Fig. 17. Penetration of subsurface light in open water, La Jolla kelp trans sect, 18 April 1957. (After Calif. State Water Quality Cont. Board 1964).

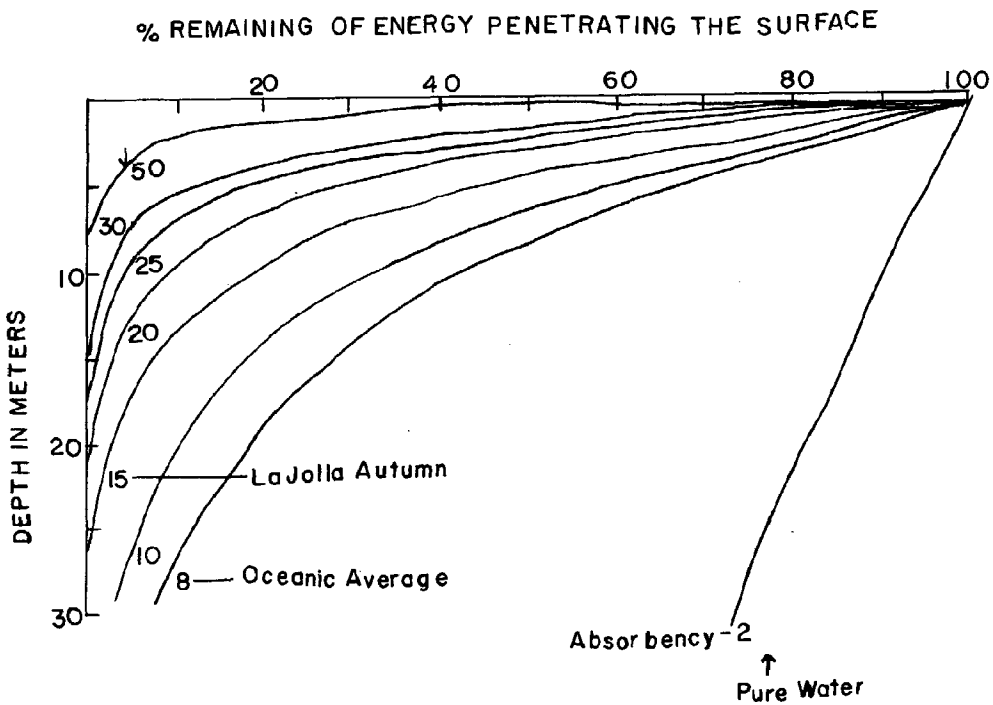

Fig. 18. Theoretical curves showing the percent of incident light remaining at any given depth for waters at different absorption coefficients (After North, 1967).

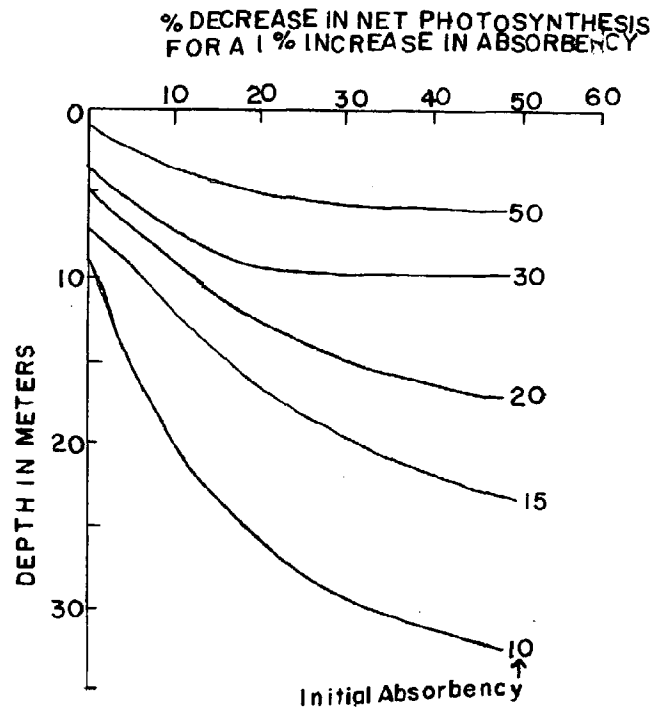

Fig. 19. Curves showing the theoretical percent decrease in photosynthesis of Macrocystis for a 1% increase in absorption coefficient, as a function of depth. Curves were determined for waters of different coefficients (After North 1958a).

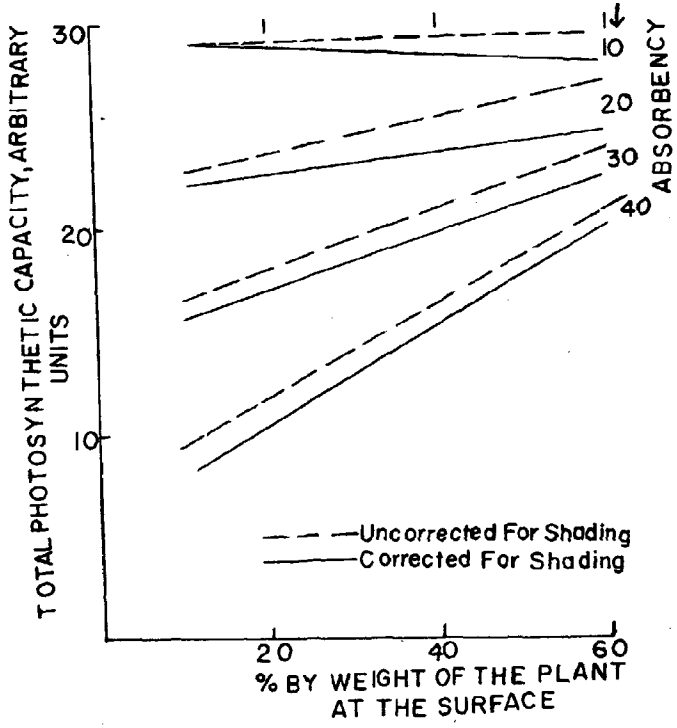

Fig. 20. Total photosynthetic capacity of kelp plants as affected by shading by surface canopy (After North 1967).

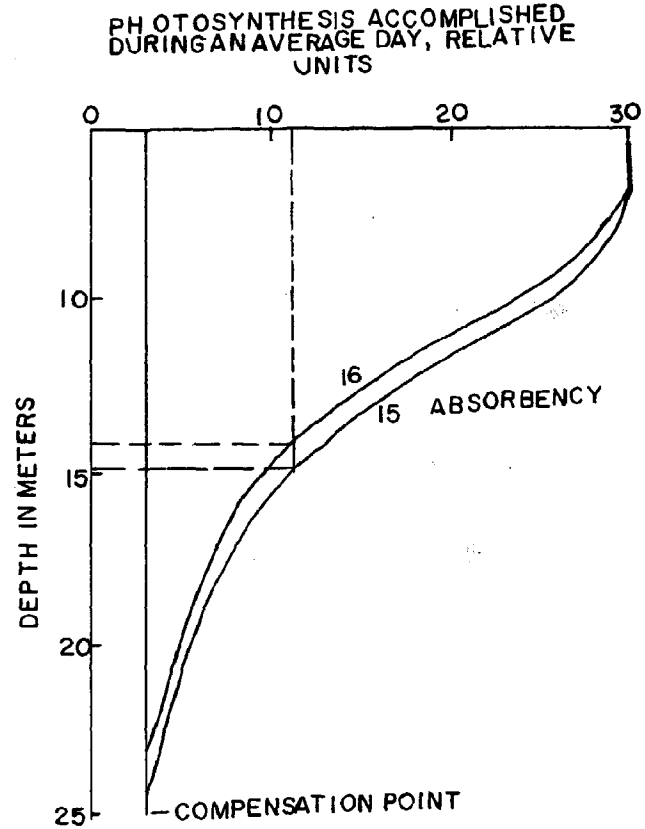

Fig. 21. Curves showing the theoretical photosynthesis of Macrocystis as a function of depth for waters of 15 and 16% absorption coefficients (After California Water Quality Control Board 1964).

of a 1% change in absorbancy on net photosynthesis. If 15 meters represented the compensation point before the change, the compensation point would be moved to 14 meters, moving the outer edge of the kelp bed shoreward. The amount of kelp affected would depend on the angle of bottom slope, but there would be a serious problem if grazer levels were high.

Figure 22 is related to disposed wastes and their effects on light in water.

Interaction of Giant Kelp System With Developing Civilization

Harvesters are allowed to cut kelp only to a depth of four feet. Owing to the amount of the plant residing in the canopy, i.e., the surface four feet, cutting could conceivably have major effects on the system. On the other hand North (1959) theorized that kelp harvesting could have beneficial effects by reducing stress on plants which might be torn loose by turbulent water. Overall he concluded that kelp harvesting was a useful substitute for a natural destructive agency, placing the resources into channels useful to man.

Studies of two types have concentrated on the possible effects of cutting. One is on the plant itself and on the growth of new individuals. The other is on the effect on the fishes.

Clendenning and Sargent (1957) found that photosynthetic rate was not affected by damaging or cutting stipes or blades. Tissue so treated continued to photosynthesize normally.

North (1967b) tested mathematical models made by combining laboratory studies with field observations in answering questions on the effect of water turbidity on photosynthesis and the balancing of loss of tissue with improvement of subsurface light intensity. North (1967b, 1968b) reported that cutting could produce stimulating or depressive changes in growth rates, presumably reflecting changes in photosynthetic capacity. Cutting in thick canopies (which yield the greatest economic returns) tended to favor stimulative changes, especially for those plants with a small proportion of tissue at the surface. He stated that the separation of long fronds from plants caused marked decreases in growth rates of the short fronds on the same plant, presumably due to the loss by translocation of energy from the long fronds in the upper lighted zone. But, cutting of plants with heavy canopies which were shading young plants should stimulate growth of the smaller plants by improving penetration of subsurface light, while temporarily reducing growth of the larger plants. He found that cutting of the upper four feet caused an initial growth retardation, but that within a month after cutting growth differences of cut and uncut plants had disappeared. Fig. 23 diagrams the loss in photosynthetic capacity when the canopy is cut at a depth of four feet.

Brandt (1923) stated that excessive cutting could reduce the yield of a bed but that infrequent harvesting, three or four times yearly, would affect the kelp beneficially. Clendenning (1968b) stated that the canopy could be harvested several times per year. This article gave a thorough review of the interrelated factors associated with harvesting. Quast (1968a) stated that normal procedures involve cutting a bed no more than three times a year. It appears that while cutting eliminates some photosynthetic capacity, it balances by stimulating growth of new plants and undergrowth of other algae. Clendenning (1968a) con-

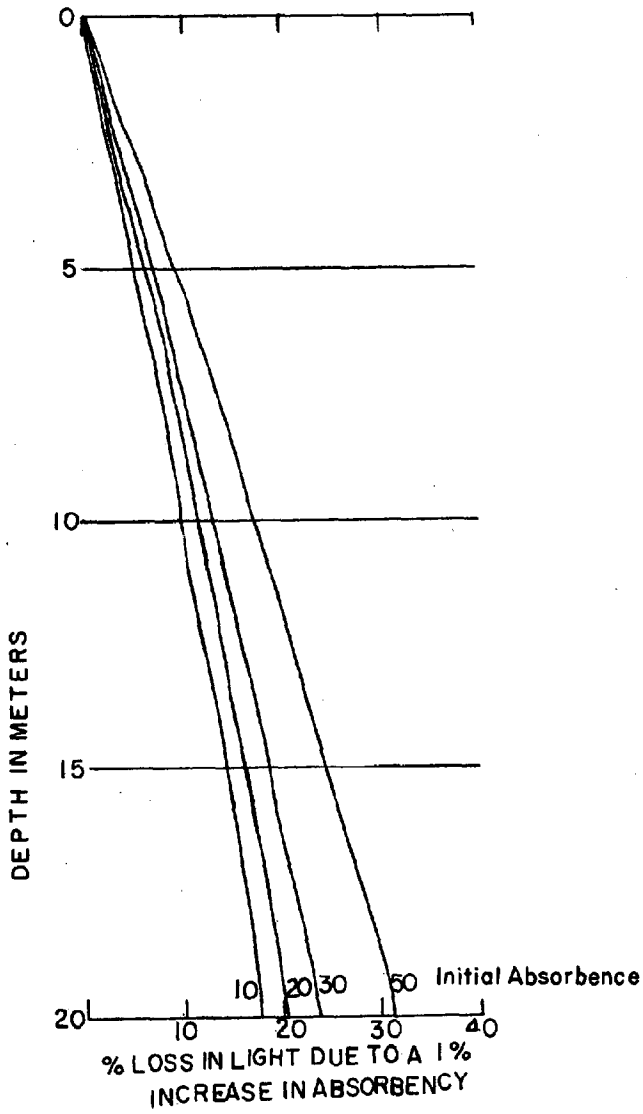

Fig. 22. Graph showing the theoretical percent reduction of light at different depths when the absorbency is increased by 1%. Curves are given for waters of different initial absorbency characteristics. (After California State Water Quality Control Board, 1964).

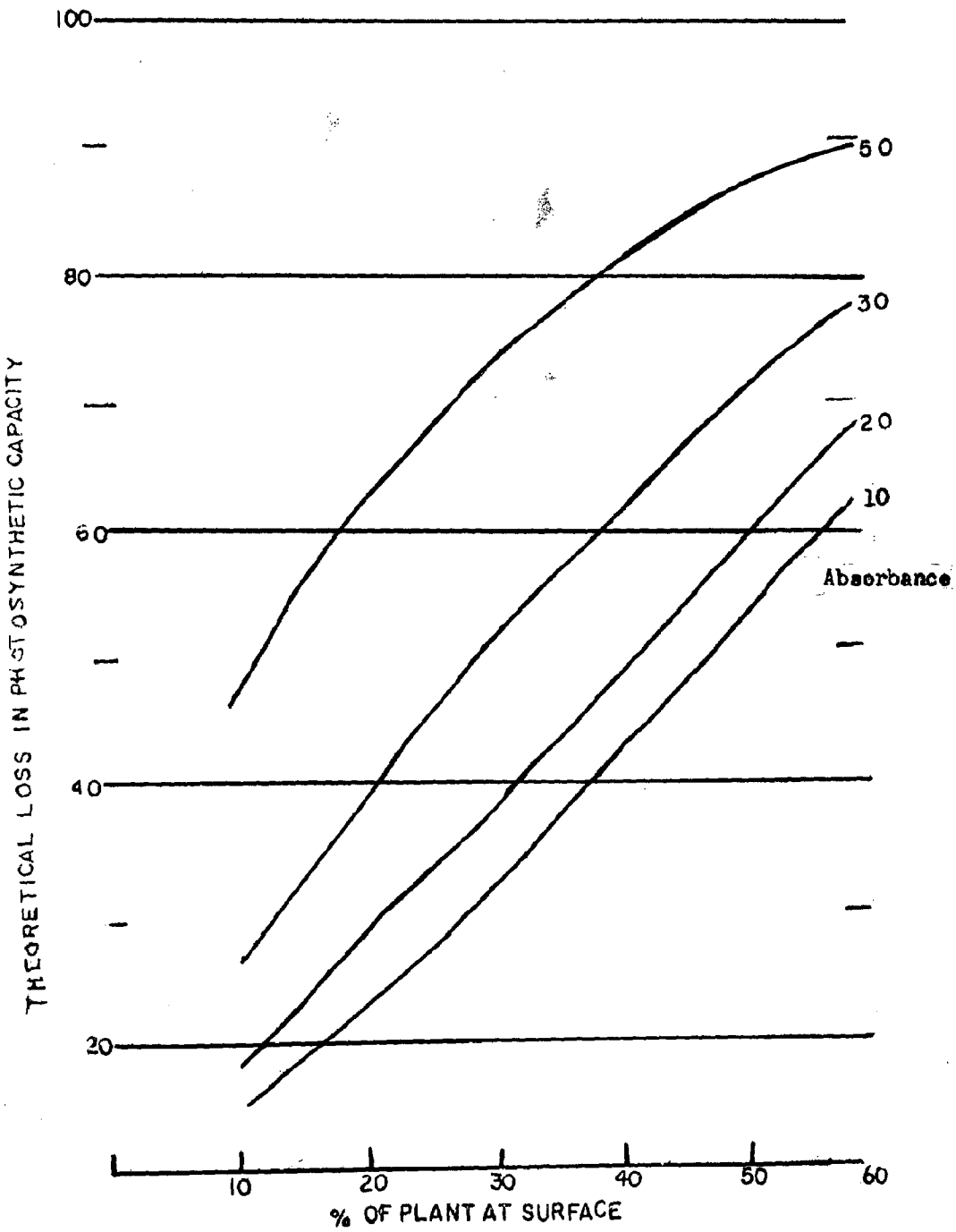

Fig. 23. Graph showing the theoretical loss in photosynthetic capacity suffered by a plant having the canopy cut off one meter beneath the surface, as a function of the percent, by weight, of the plant at the surface. Curves for different degrees of water clarity are shown. An absorbancy of 10 is very clear water and 50 is very turbid water. (After North, 1959).

cluded that unharvested beds were not those with the largest canopies. The beds with the largest yields were those harvested each year. Unharvested beds could not result in a large increase in surface canopy, owing to a frond life span of only a few months (Clendenning, 1968a).

Clendenning (1968b) estimated the number of canopy invertebrates during an actual harvest. Motile animals/m^2 of clean blade surfaces were: 545 - 640 total animals (over half were copepods, plus turbellarians, gammarid amphipods, ostracods, polychaetes, mysids, isopods, molluscs, and two fish larvae). Unharvested surface fronds collected in the area of harvest at the time of harvest yielded 6,250 - 10,800 total animals/m^2 of blades. The difference was due to the number escaping during harvest. Water draining off the conveyor of the harvestor had a total of 724 animals/U.S. gallon (over half were copepods). Six surface canopy fronds taken aboard the harvestor were examined for motile blade invertebrates. Totals were: 440,000 dropped off; 160,000 remained on the six fronds.

Quast (1968a) and Davies (1968) reported on the relation of giant kelp harvest and sportfishing. Quast (1968a) found no evidence that: harvesting destroyed eggs or larvae of fishes of actual or potential sport value, frightened sportfish from the area of harvest during harvest, removed a significant amount of fish food from a bed, or decreased the amount of fishes that could be carried by a bed. Davies (1968) reported that the frequency of harvesting had no adverse effect on sportfishing in the kelp, and that kelp-bass fishing was as good in regularly harvested beds than in uncut beds (true also for sportfishing in general). He found that when the surface temperature exceeded 75°F. (ca. 24°C.) the kelp was destroyed and pelagic fishes were attracted to the kelp beds.

Owing to imbalance in predator-prey relationships, it became necessary to control urchins populations in certain giant kelp beds (Leighton et al., 1966). Several large beds were seriously damaged while smaller beds were totally destroyed by urchins. Both chemical and manual methods were used to kill urchins. Quicklime (CaO, calcium oxide) was found to be the most practical and most suitable for use. Calcium oxide reacts rapidly with water to form calcium hydroxide, $Ca(OH)_2$ (liberating much heat), which then combines with dissolved CO_2 to form $CaCO_3$. For maximum effect the quicklime must contact the urchins within one minute after entry into the water. Thus, large lumps of chemical, 1 - 4 cm. in diameter, were used at the depths normally encountered (10 - 20 meters). Leighton et al. (1966) reported that upon contact with quicklime, urchin tissue sloughed off and infection by microorganisms occurred several days later. The amount of quicklime applied to a bed depended on depth, wave surge, bottom topography, and urchin concentrations, but generally the dosage most commonly used was 0.5 kg/m^2 (0.1 lb./ft.^{2}) with a cost of about \$.02/m^2. After urchin destruction kelps again established on the bottom.

If urchins covered an area too extensive for quicklime treatment, treatment conducted toward the restoration of kelp should be conducted only in a limited region (Leighton et al., 1966). They found that areas smaller than 5,000 m^2 were usually not successfully treated owing to inward migration of unkilled urchins and destructive grazing before new kelps could establish. They

also suggested that areas larger than 5,000 m^2 be inspected every few weeks, for urchins could build up into sufficiently dense populations along bed margins to again become harmful.

Leighton et al. (1966) found that a stable situation could exist in areas of 10,000 m^2 or larger. These areas seem to produce enough drift to satisfy urchin demands. In two cases urchins ceased foraging altogether as the drift and debris was large enough to satisfy consumption. In this way North (1968e) observed expansion of kelp into areas not actually treated with quicklime, but near areas where urchins had been brought under control.

Urchins have been manually destroyed by SCUBA divers who punctured their tests with picks, hatchets, and screwdrivers. Leighton et al. (1966) reported that 1,000 - 2,000 animals/hr. could be destroyed in this way. They concluded that manual control was not feasible when concentrations exceeded $4/m^2$ or when most of the animals were smaller than 2 cm. in diameter.

Leighton et al. (1966) intimated that sewage disposal in the vicinity of giant kelp could cause an imbalance in the plant-predator relationships. Data has already been presented which demonstrates that consumption rates can exceed plant production. This disparity is compounded by the increase in absorbance of the water as wastes are added. Thus, the urchin turns to leptopel in the waste for sustenance, and prevents a bed from returning.

It may be possible to use the sea for waste discharge, depending on the chemical content in the discharge, but it appears that the discharges can create an imbalance in the kelp system, and grazer populations can overshoot. Thus, control of grazer levels is necessary.

North has pioneered the transplantation of kelp into new areas and into areas where natural beds have disappeared. North (1968d) described a technique of moving a large number of plants at one time by tying holdfasts to a long chain, which was then towed by a boat. Transplants were reattached to permanent moorage at the transplant site. North (1968d) reported that in one experiment 124 plants were moved, and an estimated 30,000 young plants developed at the site. The reforestation of kelp quickly attracted grazers (mostly halfmoon and opaleye, extensive grazers on giant kelp) which quickly stripped all plants of blades and nearly destroyed all the young plants. North then covered the transplant area with 2-inch mesh netting which reduced the plant loss. As the kelp bed enlarged and developed, the attraction of grazing fishes into the bed reduced grazing pressures elsewhere in the area, which allowed further expansion of the bed. Thus, a fair stand of kelp was created at Whistler Reef in Orange County, California. Much more work on transplanting is found throughout North's literature, but I have picked only one good case history as an example.

Research Projects in Progress and Research Needs

As far as I am aware, the giant kelp project directed by Dr. Wheeler J. North is the only work being done on a kelp system in the United States. Chemical analyses have been made of Nereocystis, which grows from Alaska to the Monterey Peninsula, California. The plant matches giant kelp in the commercially useful products. The species is not presently being utilized, at least to any great

extent. Two things have to be considered in its use: first of all, Nereocystis is an annual plant; secondly, all blades are in the canopy with only a narrow stipe between blades and holdfast. No new plants are generated at the holdfast. In giant kelp blades are distributed along the stipe to the holdfast, with new plants constantly being produced at the holdfast. Only one harvest/year could be made on Nereocystis. One further point is that collecting costs would probably be increased using Nereocystis as urban centers are sparse along the coast where it grows. Harvesting companies in California normally collect near their processing plants to keep costs lower and to prevent chemical change in plants during the time of transportation.

North (1964b) stated that virtually no information was extant on the fate or effects of pesticides in marine waters. Research is needed in relation to the possible effects of pesticides on the giant kelp system, particularly near areas where estuaries receive drainage from agricultural or forest land.

Davies (1968) suggested that much more research be done on the correlation between fishes and kelp harvesting, and on the life history and stocks of fishes found in the kelp beds.

North (1968c) summarized eight fields which a California State Kelp Study Committee listed as deserving of further study: 1. Relation of pollution to kelp beds; 2. Effects on kelp and on fish of various methods of harvesting; 3. Expansion of beds through culturing methods; 4. Effect of kelp beds (and harvesting) on beach erosion or litter; 5. Economics of kelp and fishery values; 6. Changes in the extent and disappearance of some beds; 7. Natural causes of bed deterioration, including storms, sand movements, water turbidity, high temperatures, diseases, smothering of fronds by encrusting growths, and predation by herbivores; 8. Factors responsible for healthy growth of plants and beds.

Chapter C-12A

NEUTRAL EMBAYMENTS

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INTRODUCTION

The neutral embayment ecosystem is a partially enclosed coast environment which receives negligible river drainage and in which precipitation approximates evaporation. In general, neutral embayments are characterized by low turbidity and sedimentation rates, relatively constant salinity, and a complex pattern of seasonal variations in biota. A generalized diagram of some of the predominant organisms and their seasonal variations in a semitropical neutral embayment is presented in Figure 1. The following sections of this paper will consider the principal factors controlling the hydrography, sedimentology, ecology, and biology of neutral embayments.

HYDROGRAPHY

Salinity

The unique hydrographic feature of a neutral embayment is the lack of any significant continuous fresh water influx in a coastal environment. Thus, neutral embayments, through water exchange with the open sea, are characterized by water with oceanic salinities in the range of 28 to 36 parts per thousand total dissolved salts. The lack of significant amounts of fresh water runoff also results in a relatively stable chemical environment with only minor seasonal variations in salinity. Vertical variations in salinity, a common feature of coastal estuaries, are not found in neutral embayments. Data illustrating the salinity variations in a typical neutral embayment, Alligator Harbor, Florida (Fig. 2), are presented in Figure 3.

Temperature

The temperature regime in a neutral embayment will depend on geographic location, water depth, rates of exchange with the open sea, and the location of any artificial heat sources on the embayment. Temperature variations in shallow portions of embayments are directly related to variations in overlying air temperatures. In deeper environments water temperature is a function of both heat exchange with the overlying water mass and circulation patterns which transport water from various depths in the open ocean into the embayment. The most detailed study of thermal conditions in a neutral embayment was conducted by Skogsberg (1936) in Monterey Bay, California.

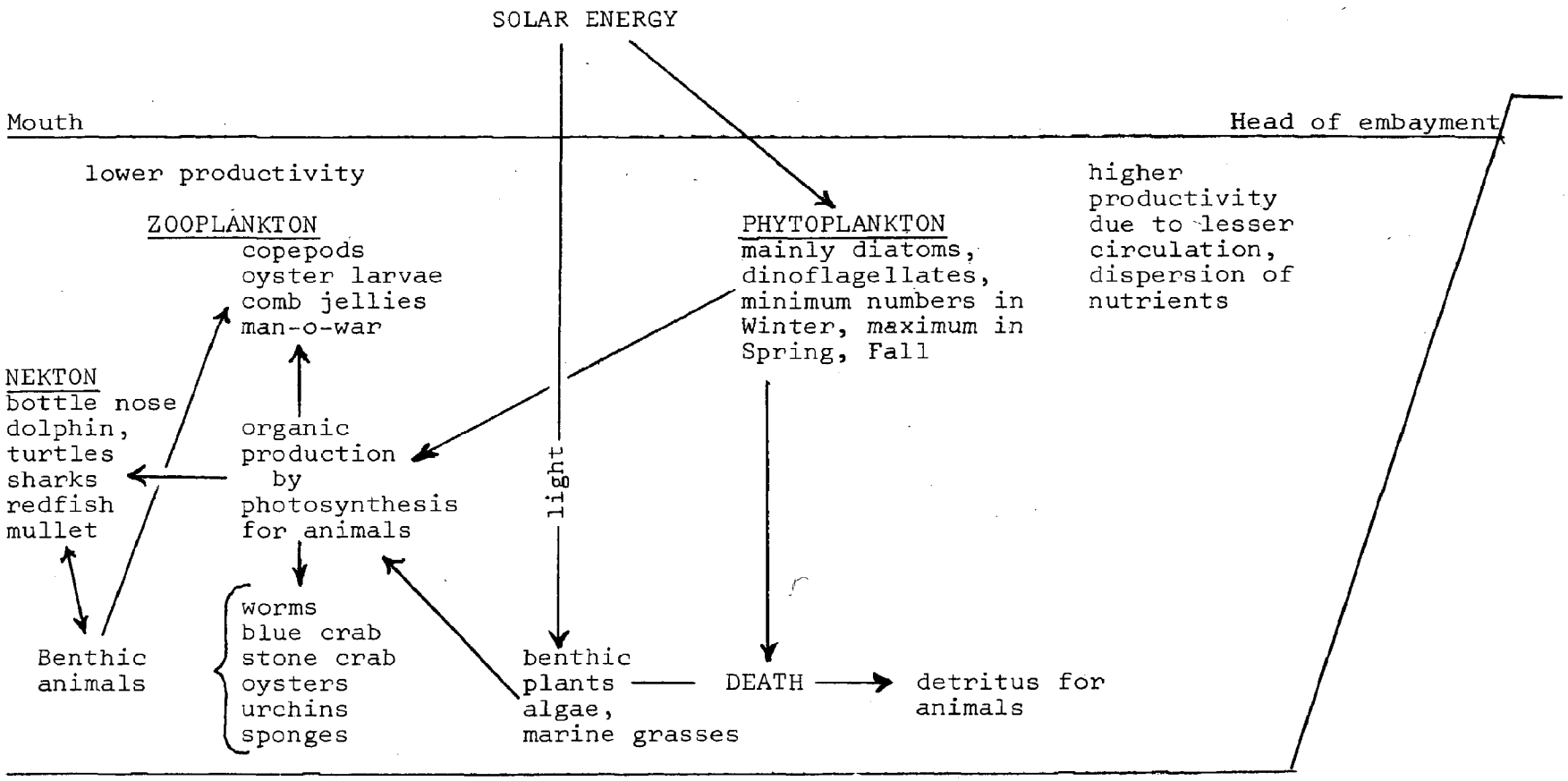
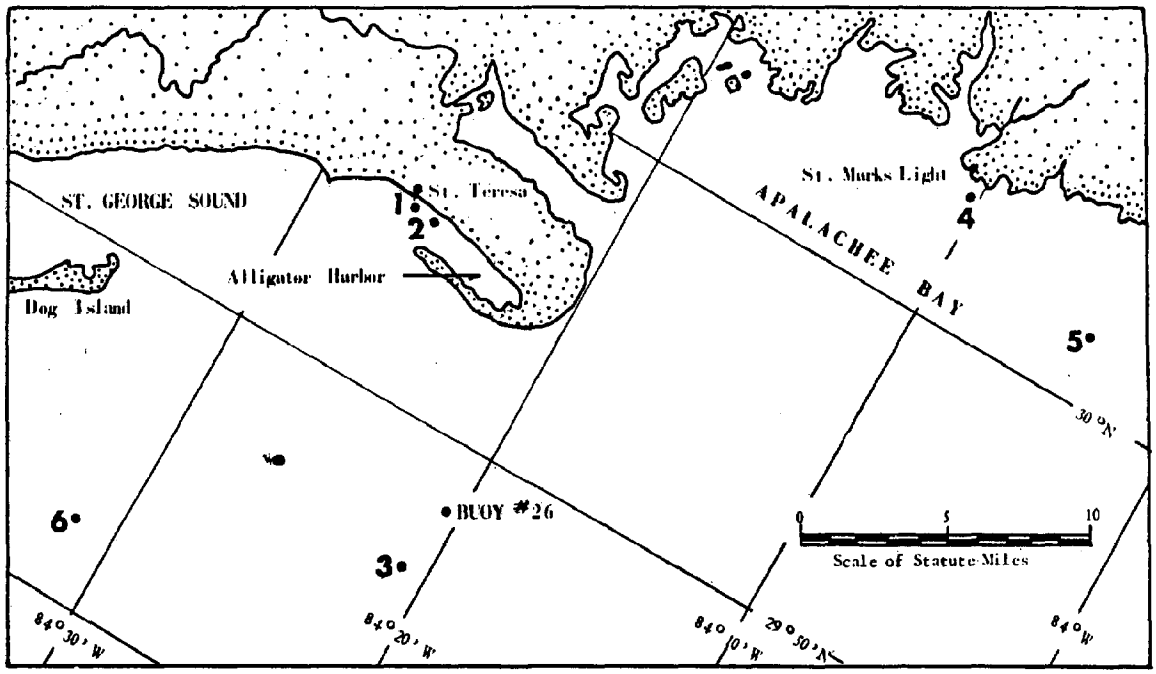


Fig. 1. Neutral embayment ecosystem as represented by Alligator Harbor, Florida.



Collecting stations of *Ostrea permollis* in the vicinity of Alligator Harbor, Florida. Numerals refer to stations.

Fig. 2. Alligator Harbor, Florida (Forbes, 1964).

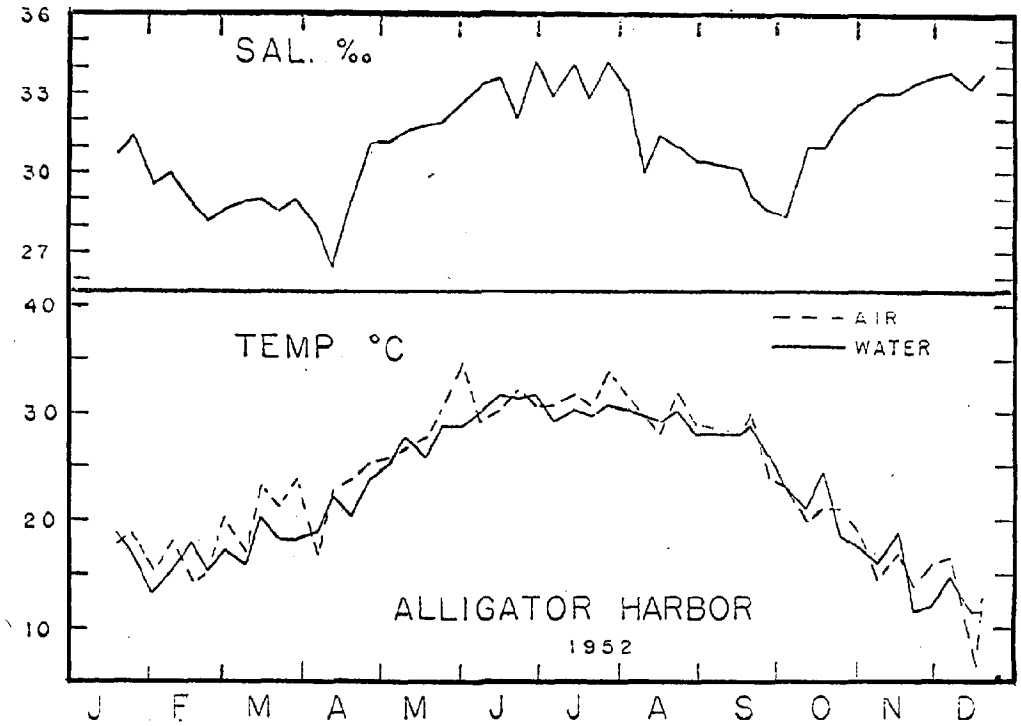


Fig. 3. Annual variations in mid-day temperature and salinity in a typical subtropical neutral embayment, Alligator Harbor, Florida (after Marshall, 1954b).

Skogsberg found a distinct annual thermal rhythm in Monterey Bay during his five year study characterized by a narrow amplitude of variation, the maximum variation at the surface being 6.5°C. The cold water season, extending from the middle of February to the end of November, is caused by upwelling of deep bottom water from the open ocean in the Bay. The warm water season results from a change in ocean currents which moves the California Current, a southerly branch of the Japan Current, closer to the coast. The narrow amplitude of temperature variation results from the upwelling of cold water during months of high air temperatures and association with a warm ocean current during months of low air temperatures. Thus, in Monterey Bay oceanographic conditions are the primary control on the thermal regime of a neutral embayment.

In contrast to Monterey Bay, Alligator Harbor, Florida, is a shallow neutral embayment located on a very wide and shallow continental shelf. In Alligator Harbor the annual temperature variation is controlled entirely by variations in air temperature. The temperature structure in this Florida neutral embayment seldom shows any stratification due to the shallow depths which result in very effective wind mixing. The annual variation in water temperature is approximately 27°C with a minimum of 8°C in January and a maximum of 35°C in July corresponding to air temperatures.

The above discussion illustrates the complexity of temperature variations in neutral embayments. Each individual embayment has a unique thermal regime. The introduction of artificial sources of thermal water from power plants and factories will have a different effect on each embayment. Therefore, prior to the construction of a source of thermal pollution on a neutral embayment a detailed survey of the currents and temperature structure of the embayment should be made for a period of at least two years to enable prediction of the patterns of dispersion and dissipation of variable amounts of thermal pollution.

Circulation

The circulation patterns in neutral embayments are primarily controlled by the interaction of the amount of wind stress on the surface, tidal changes, temperature structure, and bottom configuration of the embayment. Due to a lack of significant salinity variation the surface currents will be almost entirely a function of the direction and amount of wind stress on the water surface and the amplitude of tidal exchange with the open sea. In a deep embayment which exchanges with deep bottom waters from the open sea, such as Monterey Bay, California, thermal stratification can occur with the deep and surface currents driven by semi-independent mechanisms. Bottom currents are also highly dependent on bottom topography as demonstrated by Skogsberg (1936) in Monterey Bay, a bay dissected by a submarine valley which acts to funnel in cold water from offshore regions. Offshore winds can then displace surface water from the bay, and cold bottom water from the valley rises to the surface in an upwelling phenomenon. In a large neutral embayment such as Monterey Bay it is also necessary to differentiate between open regions of the bay and sheltered coves and harbors. In shallow coves and harbors there frequently occur local eddies in which the water is retained for periods of varying lengths and the water is often much warmer than in the open parts of the bay.

The primary consideration with respect to the ecology of a neutral embayment and susceptibility to pollution is the residence time of water in various environments in the embayment. The average residence time of water in an embayment can be calculated by dividing the volume of the embayment by the average input of water from the open sea per unit time. However, for small isolated bays within the embayment this calculation would be in error and more detailed studies would be required to determine the length of time a particular volume of water remains in the bay. Knowledge of the residence time of water in an embayment enables one to calculate the time required to discharge pollutants or utilize available dissolved oxygen for a given level of biological activity. If thermal stratification occurs in a neutral embayment then the residence time of the individual water masses must be determined in order to develop prediction models for the dispersion of pollutants. Radioactive tracers with short half lives and flourescent dyes are useful tracers for studying water movements in embayments.

SEDIMENTOLOGY

Sources and Distribution of Physical Properties

The main source of sediment to most estuaries is suspended sediment brought in by rivers. Since neutral embayments do not receive appreciable freshwater input they are characterized by lower turbidity and lower sedimentation rates than most coastal environments. The primary sources of sediment in neutral embayments is material transported in by ocean currents (i.e., longshore currents) and material derived from erosion of the surrounding land mass by wave action. The type of minerals present in bottom sediment will depend on the geology of the local area. For example, large deposits of gravel which originate from the Pleistocene glacial deposits adjacent to and exposed on the bottom of the bays are common in New England bays.

The distribution of sediment parameters such as grain size, mineral content, and carbon/nitrogen ratios is controlled by the amount of current and wave energy expended at the sediment-water interface. In shallow water environments coarse grained sediment is generally present, the fine material being removed in suspension by current activity. Fine grained mud and organic material collects in areas of very low current velocities. The distribution of sediment type and turbidity has a large influence on the ecology of benthic organisms in neutral embayments. Marshall (1954b) has demonstrated that in an unstratified neutral embayment such as Alligator Harbor, oyster larvae are dispersed over the entire area. However, the distribution of oyster bars is restricted to areas of sand where the substratum is firm.

Seasonal variability of compactness in the sediments of temperate and subtropical neutral embayments could be an important ecological factor. McMaster (1962b, 1967 demonstrated that bay sediments exhibit greater dilatancy in summer than winter. Variations in sediment compactness could effect exchange across the sediment-water interface, microbial activity in the sediment, and benthic biological activity.

Mineral-Water Reactions

The chemical dynamics of a neutral embayment are less complex than the estuarine system receiving freshwater drainage. In an estuary receiving river drainage the suspended river sediment acts as an ion exchanger during transport through the estuarine salinity gradient. The ion exchange reactions between suspended sediment and estuarine water can effect major ion composition (Nelson, 1962) and trace element balances (Kharkar et al., 1968). In a neutral embayment where sediment supply is limited and sedimentation rates slow, the minerals are not reactive and exhibit very little control on the chemistry of the system.

ECOLOGY

In Fig. 1, a neutral embayment ecosystem was described as partially enclosed marine waters, without much river flow or excessive evaporation, in which light develops a complex pattern of food chains starting with phytoplankton and benthic plants. Also, such an ecosystem has fairly constant salinity and is therefore not subject to salinity shocks. In a temperate region, seasonal changes in temperature and light are felt to be the most important ecological factors in the neutral embayment ecosystem. As will be discussed later, nutrients are also an important ecological factor since the neutral embayment does not have major inputs of both inorganic and organic nutrients from river systems such as in other estuarine types. We would then expect the neutral embayment ecosystem to be predominately under the control of marine influences as opposed to other coastal estuaries in which an interplay of marine and terrestrial factors takes place.

In terms of species composition, neutral embayments should be characterized by a high species diversity. That is to say, in such an ecosystem, there would be a relatively high ratio of numbers of different species of organisms compared to total numbers of organisms. Unfortunately, studies of diversity are made on groups of organisms as opposed to all the organisms in a estuarine ecosystem. Studies have shown that in such groups as phytoplankton, species diversity increases as one leaves estuaries and goes offshore (Hulburt, 1963). The same would be expected for other groups of organisms such as benthic invertebrates (Carriker, 1963). High diversities would be expected in neutral embayment ecosystems due to relatively uniform marine environmental conditions. In an estuarine ecosystem we would expect to find marine organisms which tolerate major reductions in salinity, often to 15% or less (euryhaline), those marine organisms that tolerate salinities down to approximately 25% (stenohaline), and those organisms classified as migrants which only spend part of their life cycle in the embayment. Those species characterized as being found in low salinities, say up to 5-10% (oligohaline), would not be expected to be found in such an ecosystem except possibly at a river mouth. A neutral embayment would be characterized as having mainly marine organisms in it as opposed to other estuarine waters which also contain fresh-water species. In fact, a neutral embayment may have the highest diversity and complexity of all temperate latitude coastal waters since they also are in the zone of coastal fish migrations.

Since rivers would exert little or no influence in the neutral embayment in terms of organic matter additions, light is the basis of all primary production in the neutral embayment. We will limit our discussion here to Alligator Harbor, Florida, which has been subjected to several ecological studies. Alligator Harbor's hydrography is mainly controlled by the excursion of high salinity Gulf of Mexico waters from Apalachee Bay which have been somewhat modified by outflow from the Ochlocknee River to the south of the embayment (Olson, 1955). Curl (1956) has shown that waters from the Apalachicola River, north of the Alligator Harbor, also influence the properties of Alligator Harbor water, but well-mixed moderate salinity (30-35%) waters enter the embayment. Where lower salinities occur, they are at the surface. Bottom waters are always of higher salinity, temperatures range from 8°C in winter to over 35°C in shallow areas during the summer (Menzel, 1957). Waters are also clear due to salting out of suspended sediments before they enter the Harbor.

A comprehensive study of the phytoplankton ecology of the region was done by Curl (1956). He found that the phytoplankton was composed mainly of temperate and warm water species of diatoms and dinoflagellates with a definite irregularity of seasonal and geographic distribution. Both spring and fall blooms were seen, with minimum cell numbers seen in the summer and winter. Curl felt that the main factors controlling primary production in the bay were 1) temperature 2) illumination, and 3) nutrients. Light was not too limiting in terms of too little an amount, but inhibition by higher light intensities was found to occur down to depths of 2 meters. In terms of nutrients, Curl felt that phosphorous was the most limiting element. Marshall (1956) studied the distribution of chlorophyll a, an index of the standing crop or amount of phytoplankton, in Alligator Harbor. He found that many of the phytoplankton in the water were members of the bottom flora which were mixed into the water as planktonic forms at the mouth of the embayment. Since he found no gradients of salinity and temperature along the length of the bay, and very slight vertical gradients, he felt that greatest concentrations of chlorophyll a were at the head of the embayment due to low dispersal rates; that is, circulation is a minimum at the head and nutrients concentrate at that point leading to increased growth. At the mouth, strong currents would cause dispersal of the populations. He also found that light levels at the surface were high enough to cause bleaching and subsequent declines of chlorophyll a. Marshall (1954) studied the distribution of oyster larvae in Alligator Harbor and found a widespread distribution of the planktonic larvae, but he found a restricted distribution of oyster bars. He felt that in a neutral embayment where plankton dispersal is relatively great, an interplay of physiographic and biological factors such as predator distribution would be the major control of where the oyster bars were located. Thus, a neutral embayment is characterized by fairly good dispersal of plankton except at the head where circulation may be restricted. This may be important in determining the dispersion of a pollutant in such an embayment as will be later discussed.

Phytoplankton are not the only primary producers in such an embayment. Six species of marine grasses are also found in the bay (Menzel, 1957) covering approximately 40% of the bottom. These act both as a food source and as a habitat for many animals from benthic invertebrates to small fish.

Also, benthic algae are present, both larger attached forms and microscopic diatoms, the so-called "mud algae." These three sets of primary producers i.e., phytoplankton, marine grasses, and benthic algae, are one of the reasons why such shallow embayments are amongst the most productive habitats on the face of the earth (Schelske and Odum, 1961). In certain Florida waters deeper than 2 meters, most of the primary production is due to phytoplankton, while above that depth, all three primary producers are of equal importance (Pomeroy, 1959,1960). Benthic plants would also supply large amounts of organic detritus which is the chief link between primary and secondary productivity (Odum and de la Cruz, 1963, 1967). Alligator Harbor has many other organisms in it. Invertebrates are very important including such commercial species as the blue crab, stone crabs, shrimp, oysters, and scallops. Fish are very numerous in the warmer months, and such commercial and sport species as mullet and spot are numerous. Some fish come in during the colder months such as the redfish. Other animals that are found in the harbor at times include bottle nose dolphins, loggerhead turtles, and sharks. Alligators are extremely rare due to poaching by man. Thus, this neutral embayment is a place where migrating fish populations spend part of their lives, mainly in the warmer months of the year. As will be mentioned later, any increases in water temperature may be detrimental to the fish populations and they may then avoid such embayments. Thermal pollution by power generating plants on such embayments might cause this.

In terms of nutrient chemistry, it would be harder to generalize upon the fertility of an neutral embayment. In the past, people have considered estuaries too fertile due to nutrients added by land drainage. Since little land drainage enters a neutral system, one could expect that it would be less fertile than other estuarine systems. A neutral embayment would also not have a two-layered flow acting as a counter-current system to concentrate nutrients in it (Ketchum, 1967b). However, work done in Georgia salt marshes (Schelske and Odum, 1961) has shown that sea water may often be higher in nutrients than river water which may indicate that certain neutral embayments may be as fertile as other estuarine areas. No work has been done, to the knowledge of the authors, on the fertility of neutral embayments, and no productivity figures were available on such ecosystems. However, one would expect neutral embayment to be less fertile than other estuaries, and the heads of such embayments may be higher in productivity than the mouths as previously discussed. Still, neutral embayments would tend to be more fertile than the open sea. Upwelling in West Coast neutral embayments such as Monterey Bay would increase their fertility.

HUMAN INFLUENCE

Perhaps the greatest interaction of man in the neutral embayment ecosystem would be in the realm of pollution. Such embayments are often in areas of high population and industrialization. In the State of California, such neutral embayments as Monterey Bay, San Pedro Bay, and Santa Monica Bay support high populations, while on the east coast of the United States, especially in the Northeast are many examples of such embayments near population centers such as Block Island Sound, Lower New York Bay, and many inlets without

rivers in Maine, Massachusetts, and New Jersey. Florida's neutral embayments such as Alligator Harbor, and Waccasassa Bay are relatively unpopulated at the present time and have little or no pollution problem.

Several pollution problems have been shown in neutral embayments. Southern California places large amounts of sewage into its adjacent embayments, and certain detrimental effects upon organisms in the area have been seen, especially benthic invertebrates (Hartman, 1956). Large oil refineries in the area present the threat of oil pollution unless careful handling of tankers takes place. Large power plants in the area also would possibly cause thermal pollution although little work has been done at the present time on the effects of such plants on neutral embayments. A neutral embayment, Bahia de San Quintin, in adjacent Baja California, is a good example of changes done by man (Barnard, 1962). In the past, otter and turtle were abundant in the bay, but human exploitation has removed all the otter, and few turtles are caught at present. A fish cannery at the head of the bay dumps large amounts of fish scraps, wastes, and blood into the waters. Tidal flushing removes and disperses most of this form of pollution and no long-term effects have been seen except for increased phosphate concentrations for several thousand square yards. The bay also has a salt industry, and recreation, especially duck hunting, is popular. If the bay was not well-flushed, pollution problems could occur from the fish wastes.

A neutral embayment that has been studied in terms of pollution has been Neroutsos Inlet in northwestern Vancouver Island, British Columbia (Waldichuk, 1958). This inlet is 11 miles long and one-half to one mile wide with an average depths of 88 meters. Very small amounts of fresh water are added by land drainage. At the head of the inlet is a sulphite pulp mill which adds, per ton of pulp made, one ton of organics and 800 pounds of digestion chemicals leading to a BOD of 650 pounds per ton of sulphite. Studies made in 1927 showed phytoplankton and zooplankton typical of sea water in the region and abundant fish, especially pilchard and salmon. Waldichuk showed that the mill has caused a major pollution problem, and mortality of small salmon and other fish has been observed. The inlet is a part of Quatsino Sound which has lots of pink salmon except in Neroutsos Inlet. Other salmon are very low in abundance in the inlet due to the pollution. The lack of significant fresh water input into the inlet does not adequately flush out the effluent from the pulp mill which is concentrated in the surface layers. Another example of poor flushing in a neutral embayment is in East Sound, Washington (Yentsch and Scagel, 1958). Here, relatively little fresh water inflow is present, which could lead to pollution problems if any pollution source was added on the Sound. Thus, neutral embayments may have serious pollution problems due to poor flushing caused by low fresh water inputs. This would be expected in embayments of a restricted, narrow physiography. Large bays, such as those in California may not be subjected to such problems if well-developed circulation patterns are present.

Recreational use of neutral embayment ecosystems in such areas as Florida and Southern California may also adversely influence such ecosystems. Vogl (1966) showed that upper Newport Bay in California was subjected to destruction by construction of boat harbors and multi-million dollar marinas. The use of small boats for recreation in Florida has added a lot of human sewage to waters and could result in health hazards and closing of certain

areas used for shellfish harvesting. No work has been published yet on the amounts of sewage added by recreational boating, but amounts could be fairly high.

Another form of pollution is thermal pollution, mainly due to the addition of heated effluents from power plants. If such a plant were placed at the head of a poorly-flushed neutral embayment, serious problems could result in terms of the ecology of the area. Again, nothing has been published on this problem in neutral embayments. Little then has been done in terms of pollution studies on neutral embayments even though they are often the site of high human activities, both domestic and industrial.

One other human interaction on such embayments which is not in the realm of pollution would be dredging and filling to construct canals, dikes, causeways, housing sites, etc. This removal of estuarine lands is especially prevalent in Florida for development of new housing and recreational sites and many conservationists have decried the destruction of the highly productive estuarine areas. Unfortunately, no work again has been done on neutral embayments as to the effects of dredging and filling of these ecosystems. Alligator Harbor is being considered as the site of a portion of the Intracoastal waterway system, and if approved, a channel will be cut into Alligator Harbor which will destroy it as a neutral embayment and convert it essentially into a lagoon separated by an offshore island.

FUTURE RESEARCH NEEDS

Neutral embayments have received very little attention relative to most coastal environments. Studies are needed on primary productivity, heat budget, nutrient cycles, and community ecology of this environment. As has been pointed out several times in the text of the present paper each neutral embayment has certain unique characteristics in circulation patterns and thermal regime. Thus, a complete oceanographic and biological survey should precede the conversion of natural resources to human use in each individual neutral embayment.

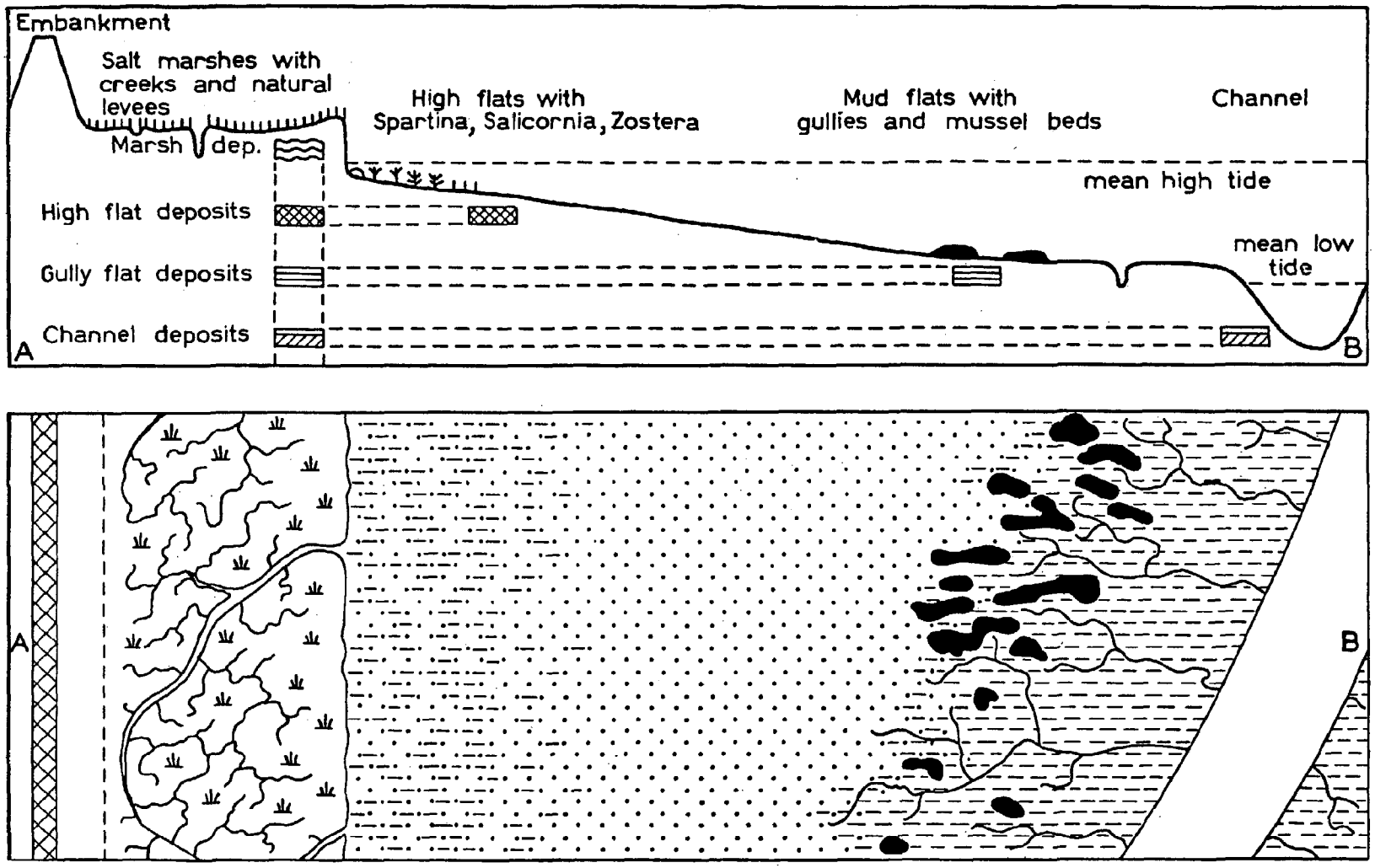


Diagram of Wadden Sea environments. Upper part: section. Lower part: map. N.B. The depth of the channels may attain more than 30 meters.

Zostera in situations with large tidal range (Van Straaten, 1959)

Chapter C-12 B

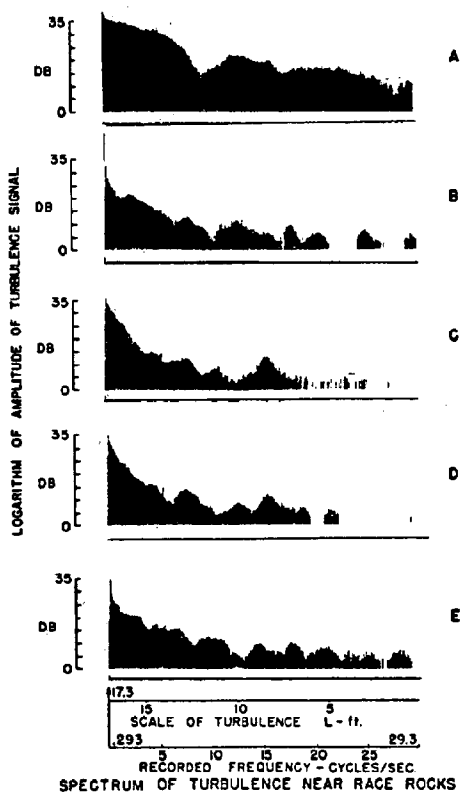
COASTAL PLANKTON

Beyond the beaches and rocks of the shore line are coastal waters over the continental shelf. With depths ranging 30 to 300 feet, photosynthetic production is mainly from phytoplankton, but a considerable fraction of the respiration and mineral cycling is accomplished by diversified bottom animals, some within the bottom and some developing on elevations exposed to strong circulatory motions from the large wave and current energies. The coastal plankton systems are the buffer between the shore and estuarine systems and the open sea where the bottom falls sharply away and the ecosystems change, the bottom subsystem being replaced by a diurnally vertical migrating complex of larger animals sometimes called the deep scattering layer because of its deflection of sound. The coastal plankton is between the estuary and the deep oceanic systems. The coastal plankton is much involved with inshore inputs and outputs, the waters moving in and out of the estuaries with the tide. The coastal system is also coupled to the estuaries by the migrating populations of shrimp, crabs, and finfish which use the estuary for a pulse of energy during nursery stages, returning to the shelf system when larger. Generally the waters in the coastal plankton system are slightly less saline than waters further out and drift to the right (as viewed by an observer facing the sea) because of the effects of rotation of the earth (Coriolis force). The coastal plankton system is the principal location of commercial fishing. In recent years, large outfalls of city and industrial wastes are being released into the coastal plankton systems, especially on the Pacific coast of the United States. The changes in the nutrient quality of these coastal waters have been much studied and there is much concern about possible effects in changing the coastal fisheries. When these high salinity waters are partly enclosed within a shore line or island archipelago, they constitute the neutral estuary (Chap. 12A) with some differences in properties of absorption of tidal energies and presence of shallow subsystems. Turbulence characteristics, measured as in Fig. 1, vary.

EXAMPLES

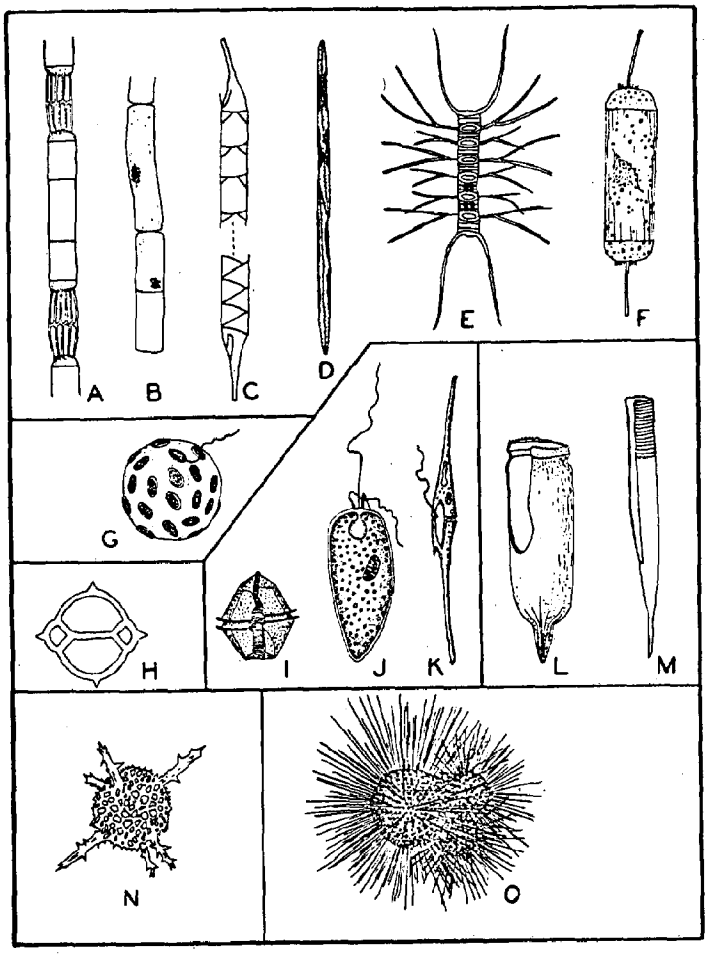
The Natural Sea Off Southern California

The coastal plankton system of Southern California is included in Emery's book (1960). With less freshwater influence than on most coasts, the system properties depend on presence or absence of upwelling of colder nutrient-rich waters. With relatively little natural stresses the diversities of the ecosystem (plankton and bottom subsystems) are sometimes almost as large as in tropical waters. From Emery (1960) are shown some characteristic plankton and seasonal records (Fig. 2). The occasional intense bloom of phytoplankton is given in Fig. 3 (Holmes, Williams, and Eppley, 1967). An energy diagram summary of processes is given in Fig. 4 (Emery, 1960).



Spectrum of turbulence in an eddy near Race Rocks.

Fig. 1. Turbulence patterns in waters (Patterson, 1958).



Common net plankton off southern California. Diatoms (×100 to ×250), from Cupp (1943): A, *Coscinosira polychorda* Gran.; B, *Leptocylindrus danicus* Cl.; C, *Rhizosolenia alata* Brightw.; D, *Nitzschia pungens* var. *atlantica* Cl.; E, *Chaetoceros decipiens* Cl.; F, *Ditylum brightwellii* (West) Grun.

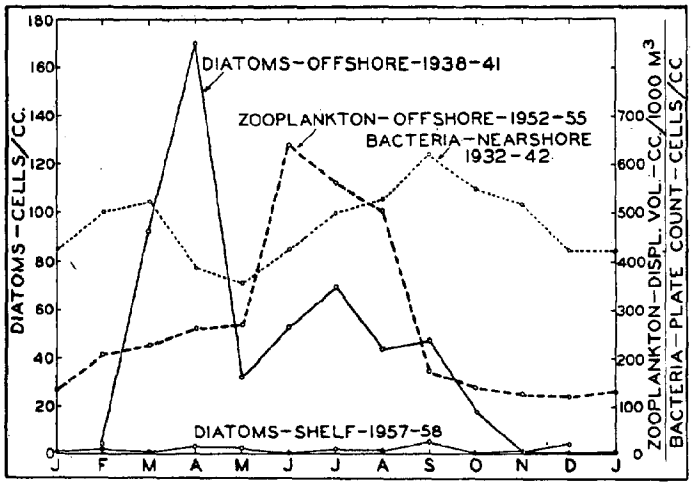
Coccolithophorid (×300): G, *Coccosphaera pelagica* Wall., silicoflagellate (×50); H, *Dictyocha fibula* Ehrbg.

Dinoflagellates (×100 to ×200), from Butschli (1883–1887): I, *Goniaulax polyhedra* Stein; J, *Porocentrum micans* Ehrbg.; K, *Ceratium fusus* Ehrbg.

Tintinnids (×60), from Kofoid and Grinnell (1929): L, *Favella franciscana* K & G.; M, *Heliocostomella subulata* (Ehrbg.).

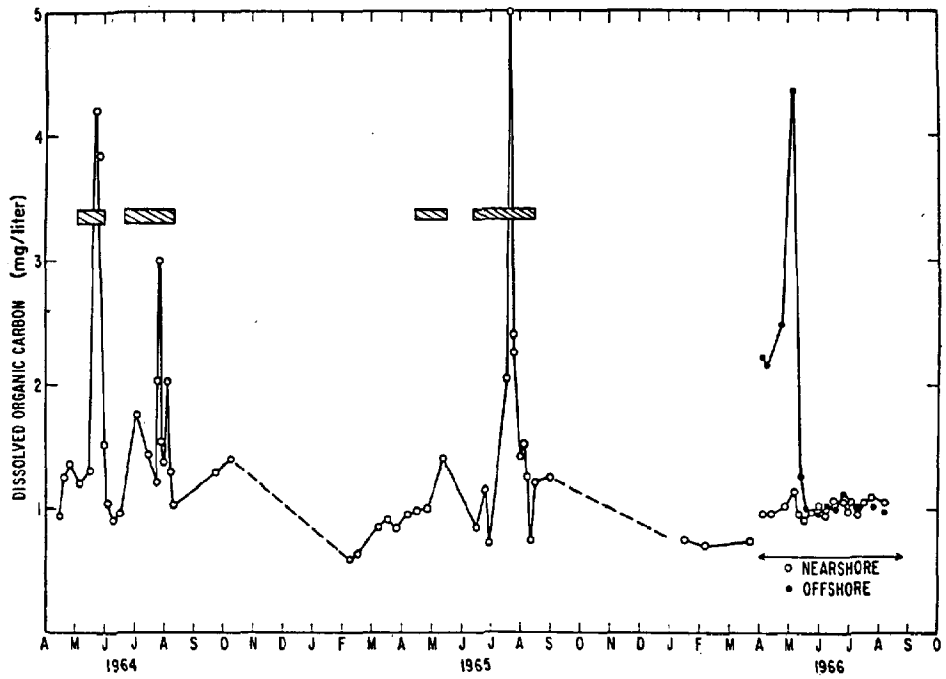
Radiolarian (rare) (×170), from Sverdrup, Johnson, and Fleming (1942): N, unknown species.

Foraminifer (×25); O, *Globigerina bulloides* d'Orbigny.



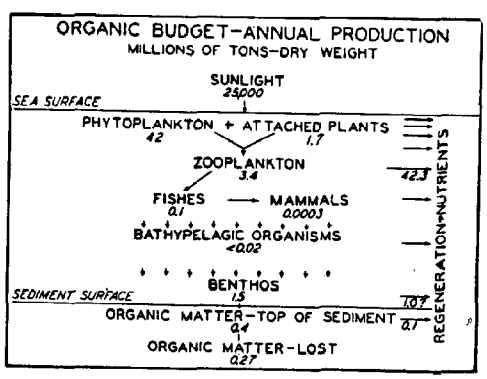
Average monthly abundance of diatoms and zooplankton. Diatom counts (cells per cubic centimeter) for the offshore area are averages of concentrations measured by Allen during 1938–1941 at 0, 20, 40, and 60 meters (Sverdrup and Staff, 1942, 1943, 1944, and 1947). Those for the shelf area were measured by Resig during 1947 and early 1958. Zooplankton concentrations (displacement volumes in cubic centimeters per 1000 cubic meters) were measured during 1952–1955 by the Staff, South Pacific Fisheries Investigations (1953, 1954, 1955, and 1956), from oblique tow net hauls between 140 meters and the surface. Bacterial concentrations (cells per cubic centimeter) are from plate counts reported by ZoBell (1946*c*, p. 75) for collections at the pier end at Scripps Institution of Oceanography during 1932–1942. Note the lag of greatest concentration of zooplankton and bacteria after the peak concentration of diatoms. Because the bacteria were collected over quite shallow water (about 6 meters), their abundance may be controlled more by the presence of bottom sediment stirred up by seasonal waves than by the presence of organic debris.

Fig. 2. Plankton basis of the coastal waters off Southern California (Emery, 1960).



Variation in dissolved organic carbon content of surface water collected at Scripps pier, April 1964 through March 1966, and at stations 0.8 km (open circles) and 3.2 km (solid circles) offshore of Scripps pier April–October 1966. Hatched bars indicate times of red water.

Fig. 3. Blooms off Southern California (Holmes, Williams, and Eppley, 1967).



Approximate flow chart of organic matter and annual production of the various biozones of southern California.

Fig. 4. Energy flow off Southern California (Emery, 1960).

Diversity among crustacea is graphed by Barnard and Jones (1960) in Fig. 5. Many papers show the substitution of species with depth and other local differences, dividing up the bottom food opportunities with many subsystems specialized for slightly different conditions.

Sewage Outfalls Off Southern California

Examples of the change in the coastal plankton system (and its bottom subsystems) produced by outfalls of sewage wastes are documented for Orange Co. Santa Monica (Hyperion), Los Angeles County, Santa Barbara and others. As shown in examples in Figs. 6-10 and Table 1 there are differences recognizable at distances of several miles. As the number of these outfalls has risen, the general levels of turbidity, nutrients, and subtle effects causing changes in micro-organism populations may have become general on this entire coast.

Shelf off West Coast of Florida

Receiving highly irregular injections of freshwater and wastes from peninsula Florida the broad shelf off the west coast (Fig. 11) supports a plankton based system that draws intense public interest from time to time as red tide blooms develop. Gymnodinium breve is the red tide organism in these waters and is poisonous, causing fish kills (Fig. 12). Bloom conditions are given in Fig. 13. Composition of phytoplankton bloom further north is given in Fig. 14. A new fishery developing here is the thread herring (Fig. 11). Have the numbers increased with the nutrient levels? Also irregular are the ups and downs in the sponge harvesting industry on this coast.

Coastal Waters of Maine

On the coast of Maine strong tidal flows sweep in and out among coastal islands, peninsulas and drowned valleys. Moving seaward from rivers one passes to deeper bottoms and broader expanses of coastal water until finally the bottom drops away under open water of the Gulf of Maine. A series of plankton studies by Sherman (1965, 1966a, 1966b, and 1968) documents a coastal plankton system between the inshore estuarine characteristics and the open sea. Acartia, characteristic of the middle salinity estuarine system (Chap. C-9), grades into Pseudocalanus and then Calanus offshore. (See Tab Fig. 15a,c,d. The coastal plankton zone has the alewife as principal zooplankton eating fish. Glover (1961) defines the seaward side of the coastal plankton zon (Fig. 15b).

South Atlantic Coastal Waters

The zones of coastal water exist along the south Atlantic coasts of the Carolinas and Georgia between the estuaries and the Gulf Stream. Arrowworms (Chaetognatha) are carnivorous zooplankton organisms that have been used as water mass (ecosystem) indicators throughout the world. In Fig. 16 arrowworms (genus Sagitta) are mapped showing the zones of the coast recognizable by changing species with depth.

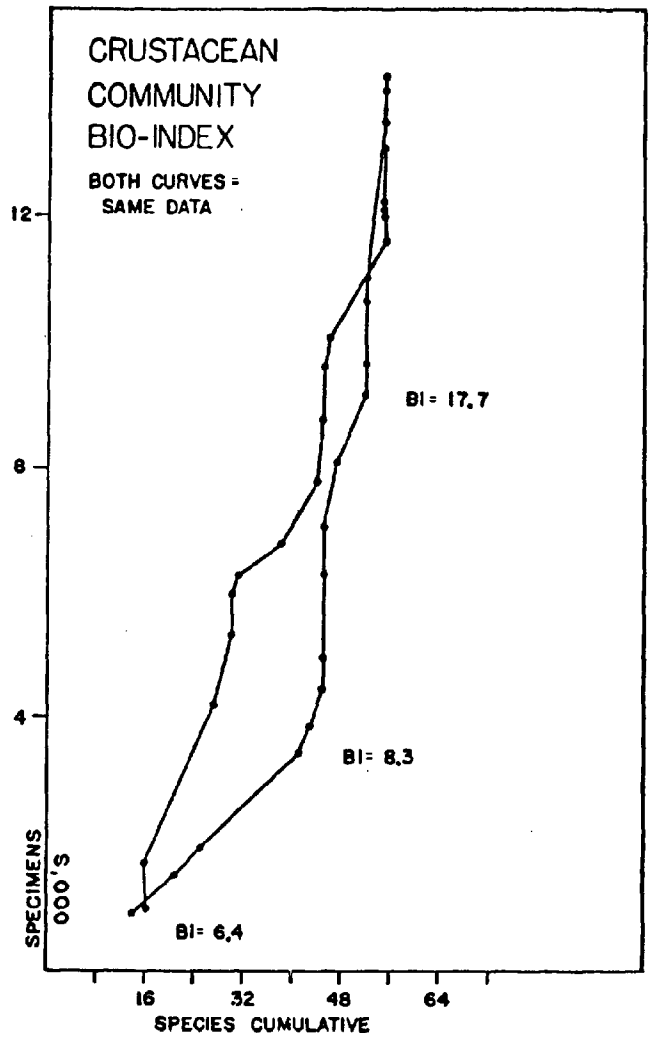
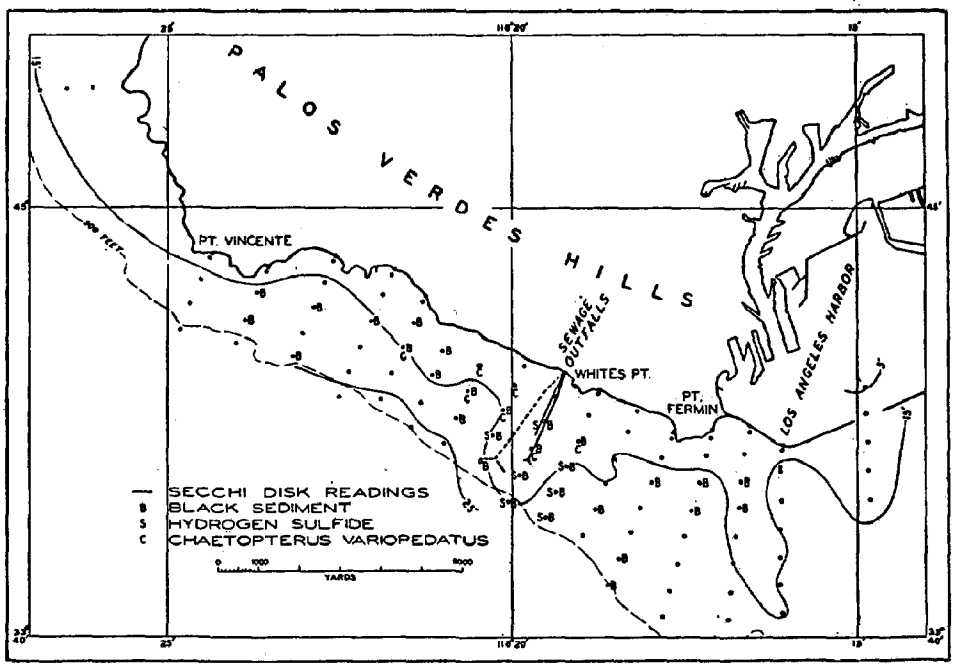


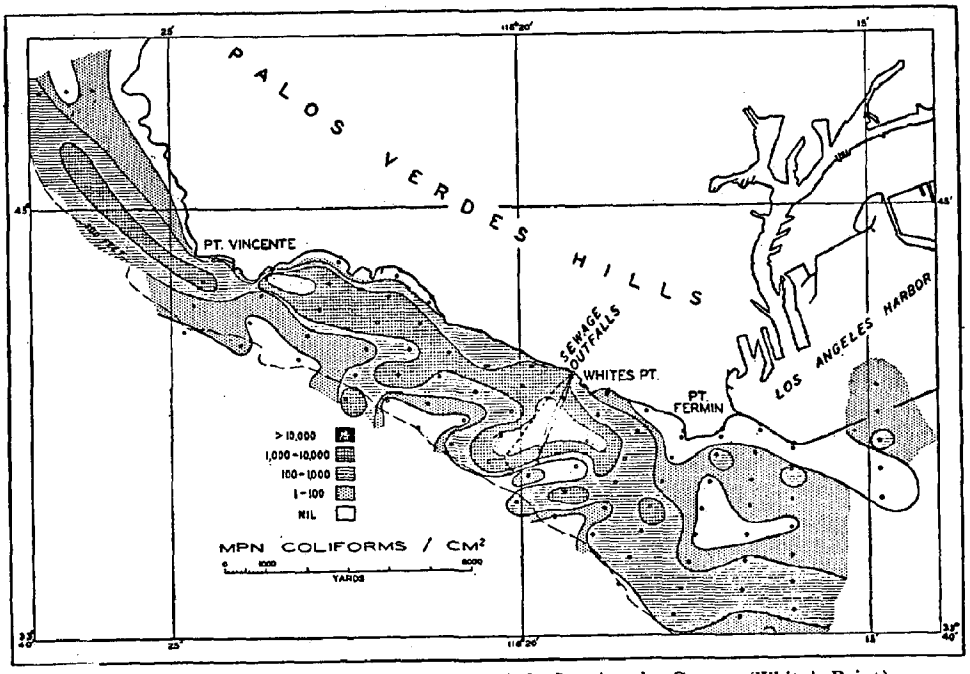
Fig. 4.

Bio-index analyses of a crustacean community on the Santa Barbara shelf.

Fig. 5. Diversity off Southern California (Barnard and Jones, 1960).

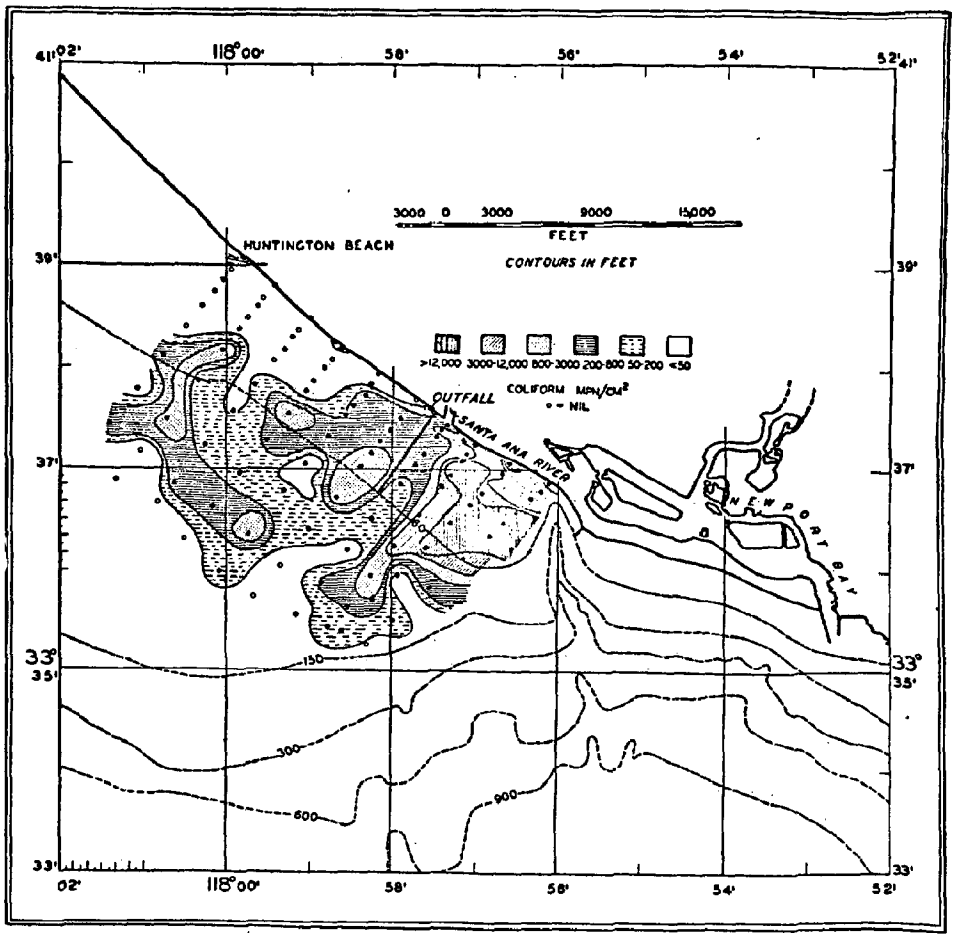


Distribution of black sediments, hydrogen sulfide, and *Chaetopterus variopedatus* in the vicinity of the Los Angeles County (White's Point) sewage outfall.



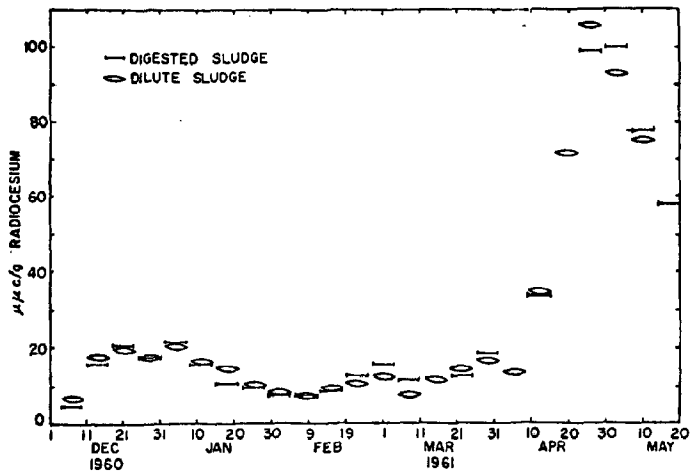
Coliform bacteria in the sediments around the Los Angeles County (White's Point) sewage outfalls.

Fig. 6. Bottom worms(Chaetopterus), sludge, and intestinal bacteria off Southern California (Rittenberg, Mittwer, and Ivler, 1958).



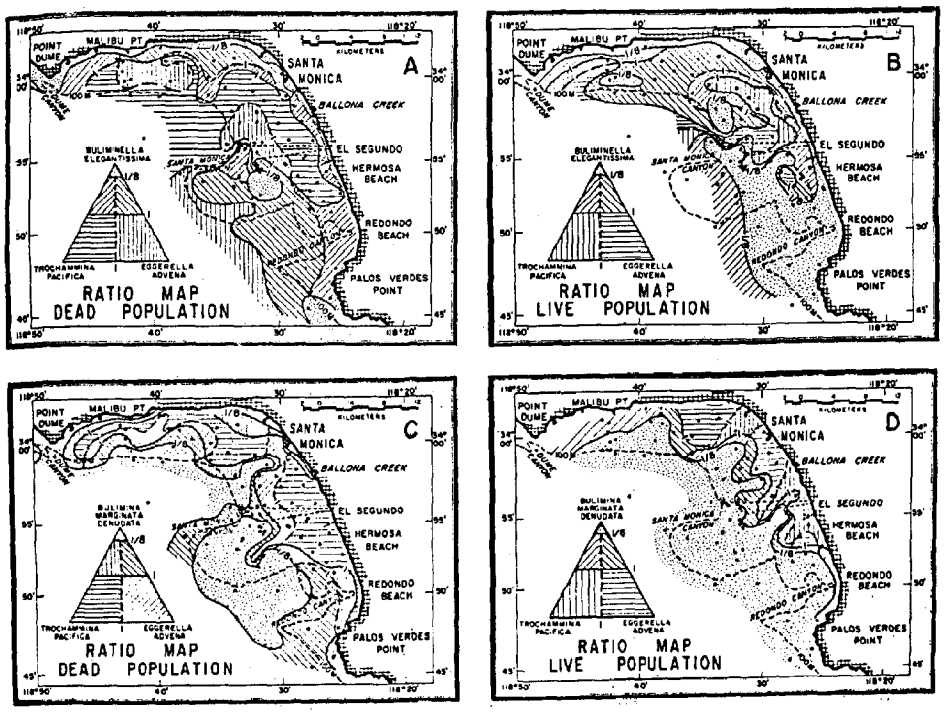
Coliform bacteria in the sediments around the Orange County sewage outfall

Fig. 7. From Rittenberg, Mittwer, and Ivler (1958).



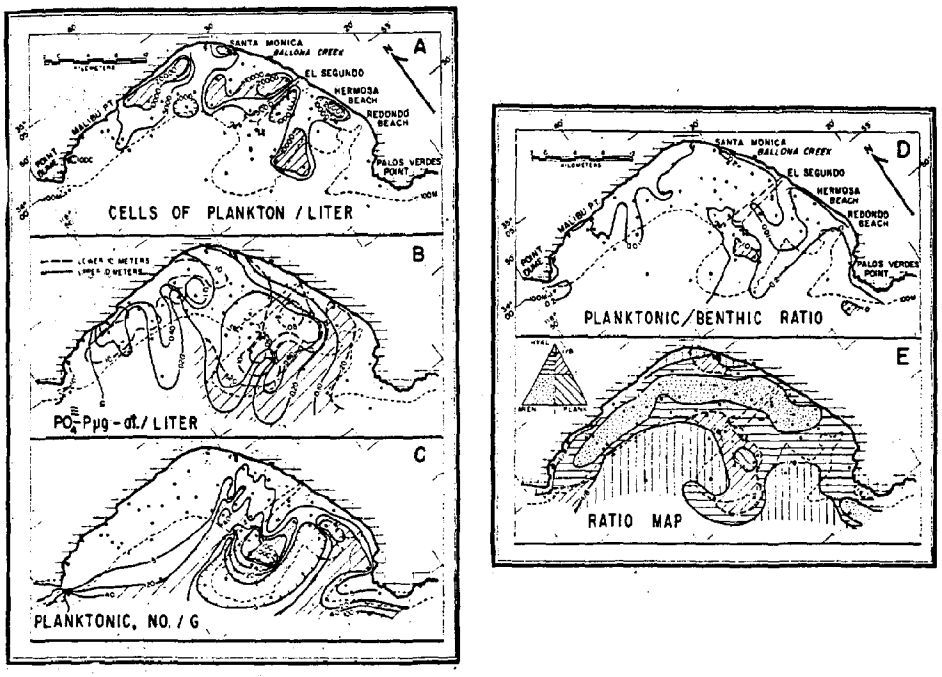
—Radiocesium activity in Hyperion digested and dilute sludges (Dec. 1960–May 1961).

Fig. 8. Radioactive isotopes emerging in Sewer off Southern California (Folsom, Mohanrao, Betz, and Garber, 1965).

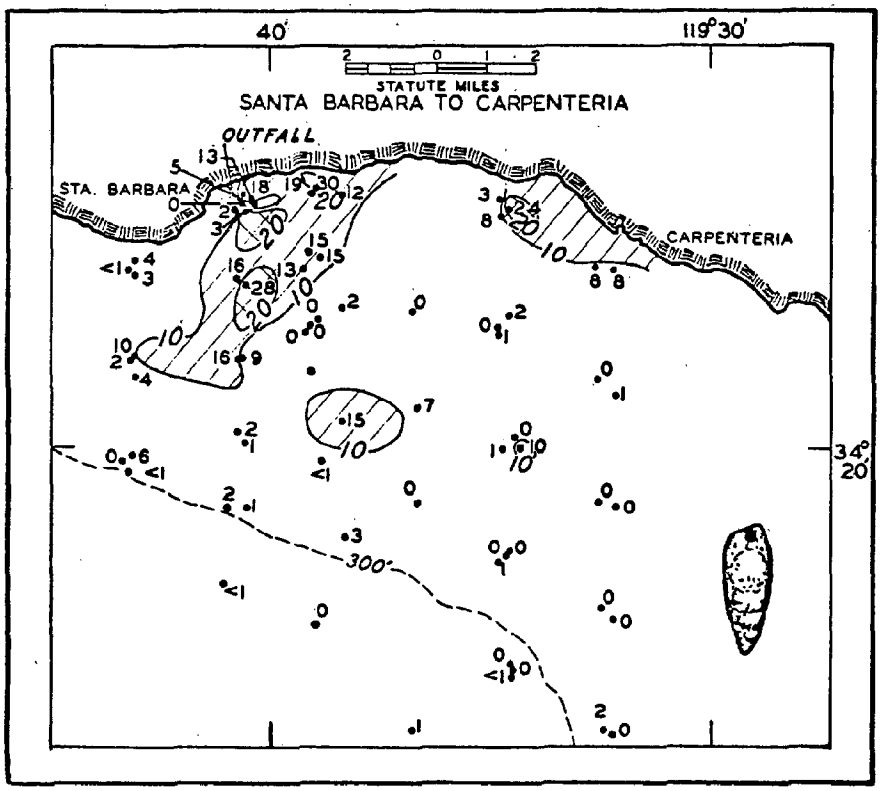


Trigon plots of dominant species in the outfall area. Distribution of *Buliminella elegantissima* d'Orbigny-*Trochammina pacifica* Cushman-*Eggerella advena* (Cushman) in the A. Dead population, B. Live population. Distribution of *Bulimina marginata denudata* Cushman and [illegible]rker-*Trochammina pac[illegible]fica* Cushman-*Eggerella advena* (Cushman) in the C. Dead population, [illegible]ve population.

Fig. 9. Patterns in water and on the bottom off Southern California in relation to offshore sewage outfalls (Bandy, Ingle, and Resig, 1965b).



Planktonic relationships. A. Cells of plankton/liter, maximum for the water column. B. Phosphate in μg-at./liter in the upper and lower 10 m of the water column. C. Number/g of planktonic specimens in bottom sediments. D. Planktonic/benthic foraminiferal ratios. E. Trigon analysis of planktonic-arenaceous-hyaline benthic foraminiferal groups. Note higher values for planktonics in outfall area.



Eggerella advena

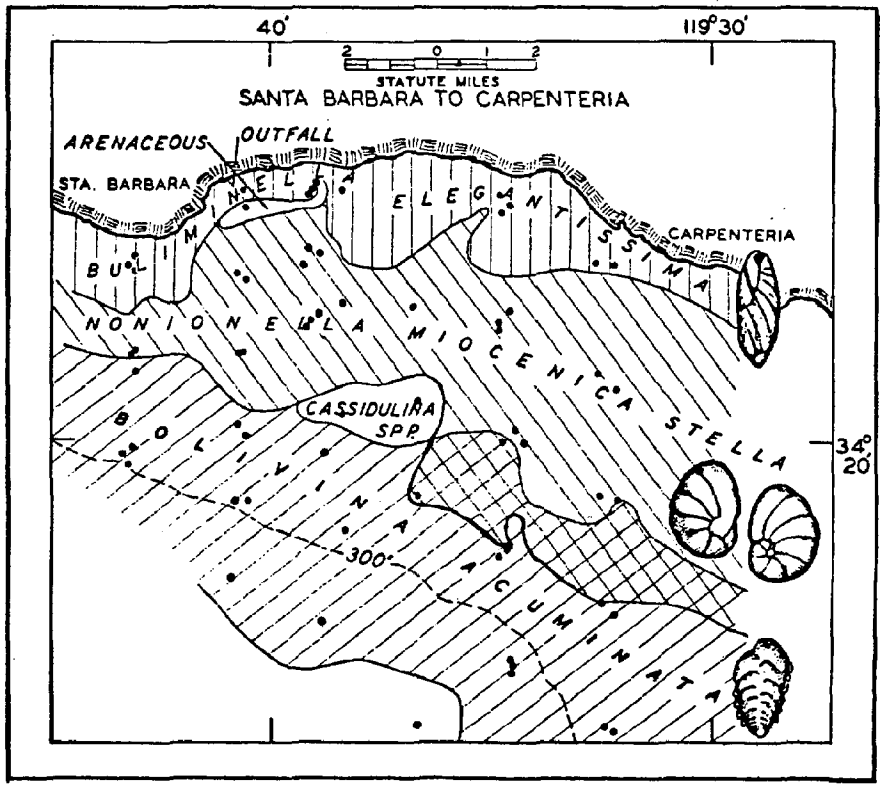


Fig. 10. Foraminifera off Santa Barbara, California (Resig, 1960).

Table 1. Benthonic fauna off Southern California (Hartman, 1960)

A summary of depth of bottom, with weights of dominant animal groups and distance from Santa Monica light follows:

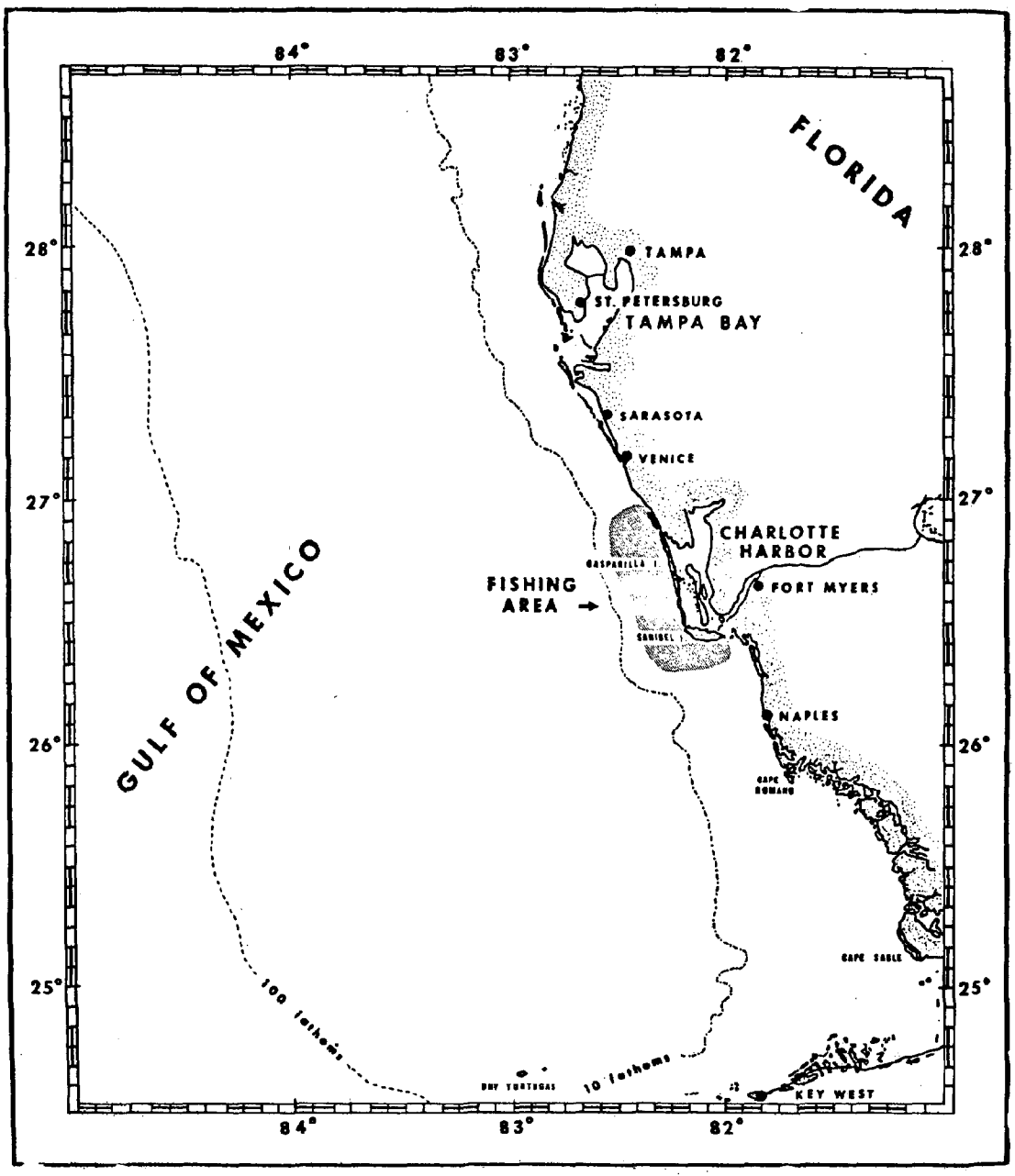
depth in ft.	weights in grams of largest and/or dominant animals by sample	distance from Santa Monica light in miles
30 ft.	polychaetes, 1.9 g; mollusks 0.3 g	2.55
33 ft.	Astropecten, 31 g; polychaetes 3.5 g	0.3
42 ft.	polychaetes with Glycera, 5 g; crustaceans 0.6 g; mollusks 0.4 g	4.85
57 ft.	crab, 7.1 g; Polinices, 4.7 g; polychaetes 3.1 g	10.95
107 ft.	Glycera robusta, 7.2 g; Diploma, 1.6 g; other mollusks, 4.6 g; ophiuroids 3.8 g	7.25
116 ft.	Pseudopotamilla, .. g; sea whip, 3.6 g; ophiuroids, 5.7 g	10.7
157 ft.	ophiuroids, 12.2 g; polychaetes 6.1 g; sea whip, 2.1 g; mollusks, 1 g.	7.1
160 ft.	ophiuroids, 20 g; Travisia and Pherusa, 7.3 g; mollusks, 1 g; enteropneust, 1 g.	10.3
220 ft.	Amphiodia urtica, 39 g; brissopsids, 7.5 g; polychaetes, 4.1 g; sipunculids, 3.8 g.	4.9
225 ft.	Amphiodia urtica, 97.2 g; polychaetes 2.3 g; nemerteans, 1.2 g.	10.1
441 ft.	Amphiodia urtica, 34.5 g; polychaetes with Travisia, 23.4 g; crustaceans, 0.9 g.	8.0
490 ft.	Otophidium (fish) 24.9 g; ophiuroids, 19.7 g; Brisaster, 11.8 g; polychaetes with Travisia, 11.8 g.	9.85
500 ft.	brissopsid, 47.9 g; ophiuroids, 1.9 g; polychaetes, 1.2 g.	9.3
1330 ft.	Arynchite (echiuroid) 14.8 g; brissopsids, 6 g; polychaetes, 5.5 g; mollusks, 1 g.	10.0

A similar summary for distances from Hyperion stack follows:

38 ft.	Astropecten, 3.3 g; polychaetes, 1.8 g; Polinices, 0.2 g; other mollusks, 0.4 g.	1.8
92 ft.	Megasurcula, 15.1 g; Astropecten, 11.5 g; polychaetes, 3.8 g.	2.75
158 ft.	polychaetes, 6 g; nemertean, 0.9 g; mollusks, 1.6 g; Randallia (crab) 0.4 g.	3.3
232 ft.	Amphiodia urtica, 20.1 g; polychaetes 3 g; Leptosynapta albicans, 1.1 g; nemerteans, 0.7 g.	4.4
217 ft.	polychaetes, 1.7 g; crustaceans, 0.6 g; nemerteans, 0.6 g.	6.35
515 ft.	brissopsids, 29.6 g; ophiuroids, 14.9 g; polychaetes, 7.8 g; mollusks, 3 g.	8.45

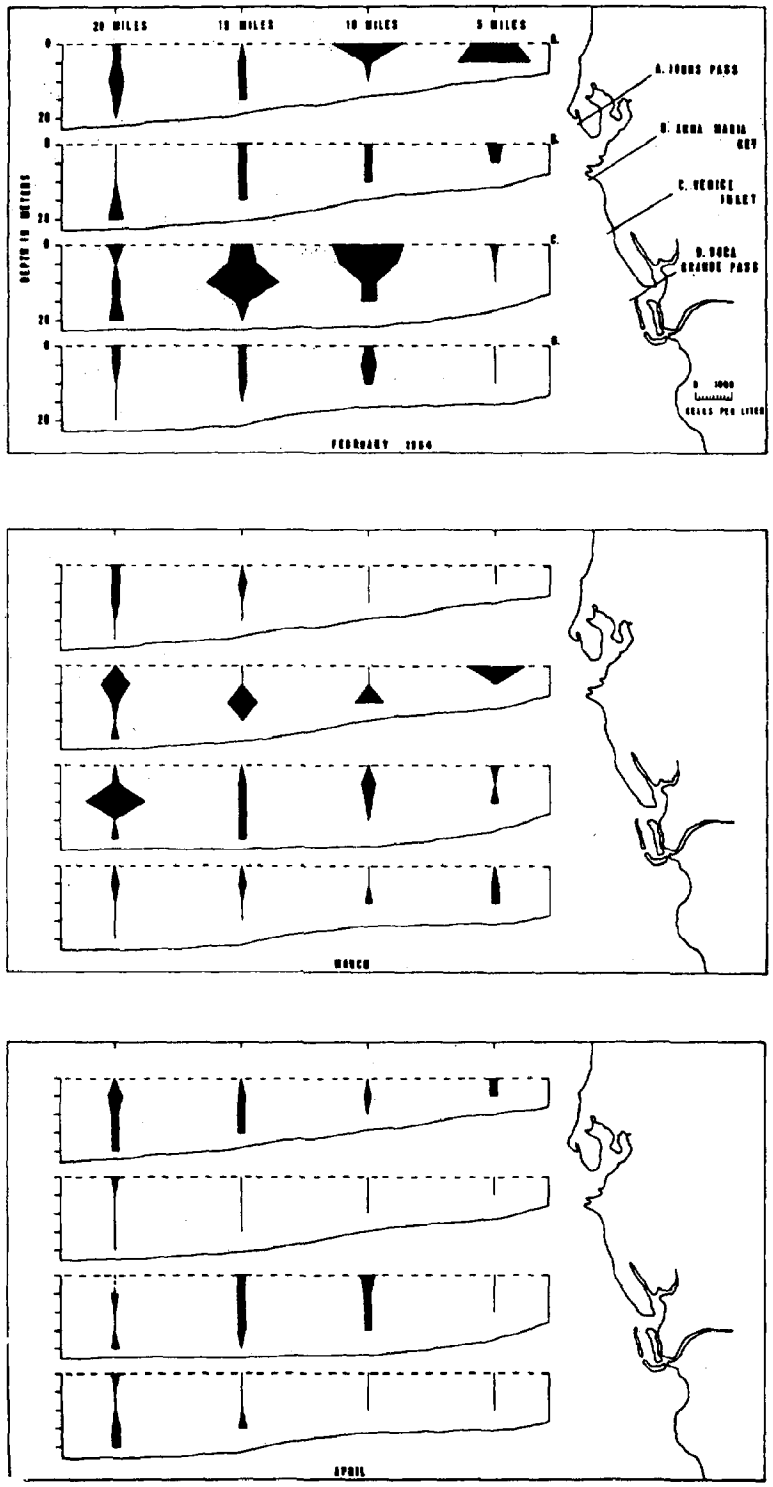
A comparable result is expressed in the following, in which distance is from Hyperion stack, giving numbers of species and specimens in a sample, and kind of sediment for each:

1.4 mi, with 78 species and 1065 specimens, in very coarse black sand.
3.0 mi, with 131 species and 1020 specimens, in olive-green silty sand.
3.0 mi, with 113 species and 1331 specimens, in green silt.
5.7 mi, with 135 species and 1009 specimens, in green sand with gravel.
5.75 mi, with 115 species and 1683 specimens, in olive-green silty sand.
6.0 mi, with 98 species and 432 specimens, in rocks, sand and gravel.
8.75 mi, with 123 species and 1041 specimens, in green sity sand and rock.



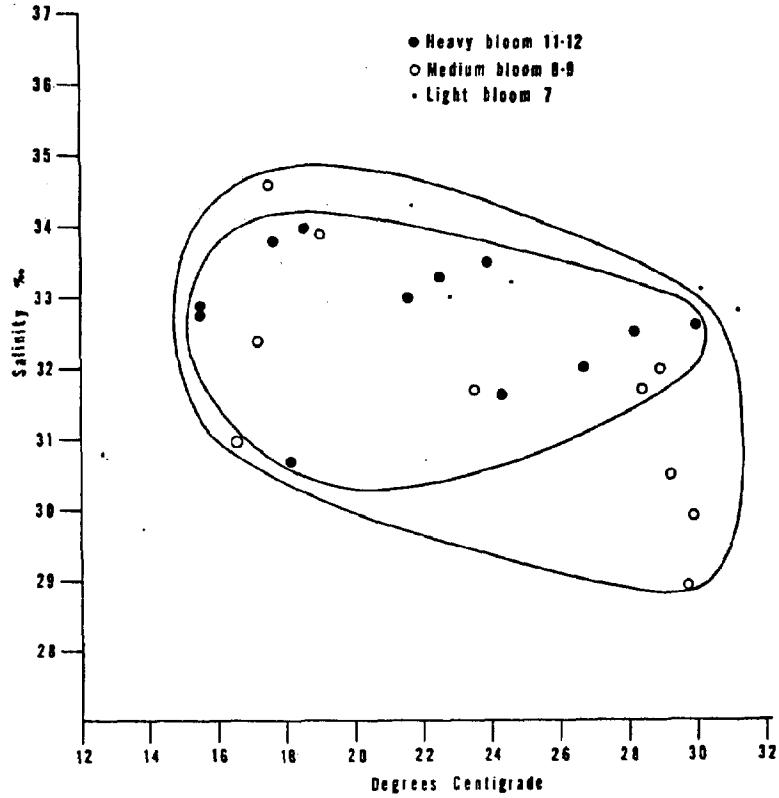
Thread herring fishing grounds on Florida west coast.

Fig. 11. Shelf plankton system off the west coast of Florida (Fuss, 1968).



--Vertical and temporal distribution of G. breve at sampling areas along the west coast of Florida.

Fig. 12. Red tide flagellates off the West coast of Florida (Dragovich and Kelly, 1966).



Mean monthly abundance rankings of *G. breve* for bloom stages versus temperature and salinity.

Fig. 13. Florida Red Tide Blooms (Rounsefell and Dragovich, 1966)

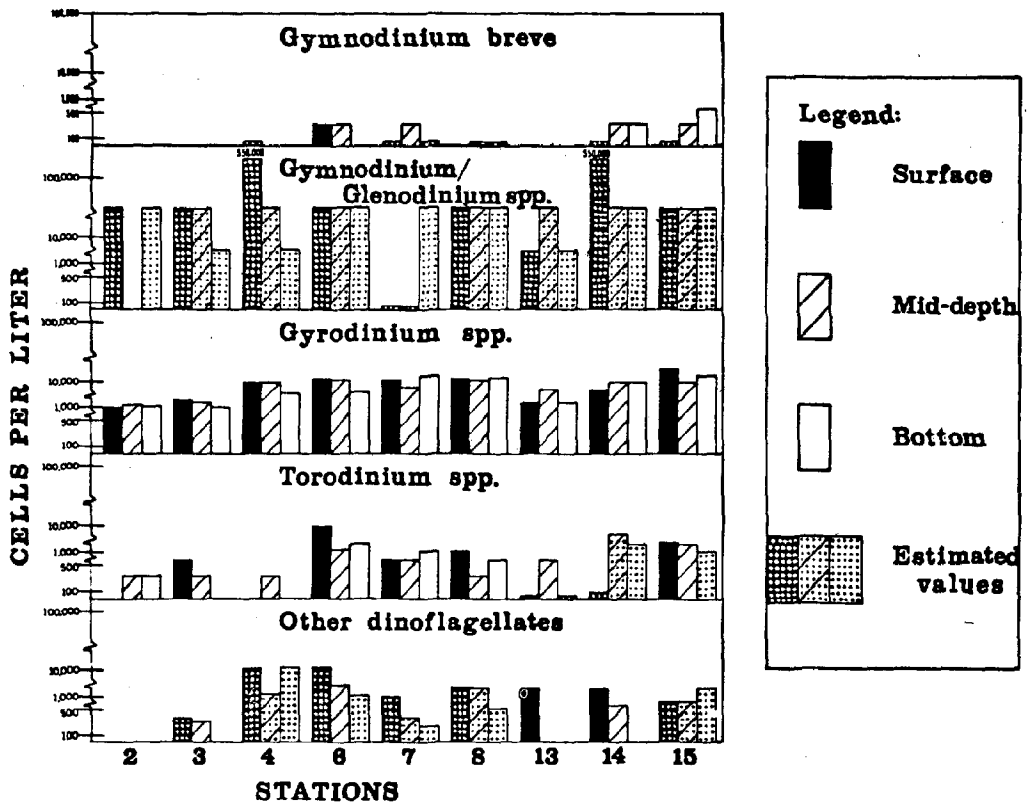


Fig. 14. Red tide and other organisms in Apalachee Bay, Fla (Streidinger, Davis, and Williams, 1966).

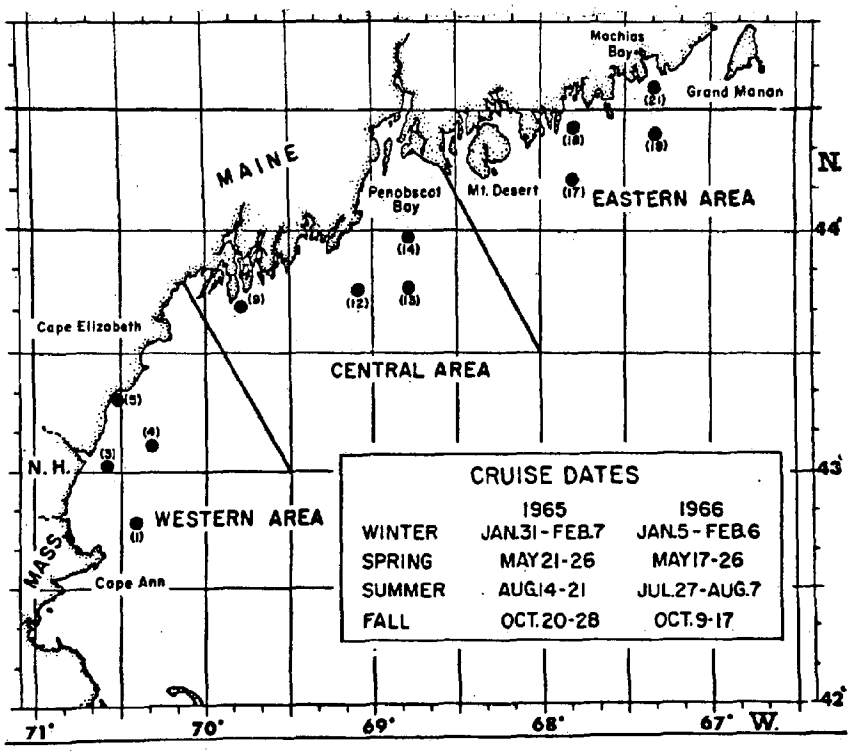
Table 2.

Copepod species in zooplankton samples, Gulf of Maine coastal waters, 1965 and 1966

1965		1966	
Species	Mean number/ 100 m.^{3}/ station	Species	Mean number/ 100 m.^{3}/ station
Common species (>50/100 m.^{3})		Common species (>50/100 m.^{3})	
Calanus finmarchicus (Gunnerus)..	8,934	Calanus finmarchicus (Gunnerus)..	3,749
Temora longicornis (Muller).....	600	Centropages typicus Kroyer.....	680
Centropages typicus Kroyer.....	257	Pseudocalanus minutus (Kroyer)...	182
Pseudocalanus minutus (Kroyer)...	204	Temora longicornis (Muller).....	114
Metridia lucens Boeck.....	88	Oithona similis Claus.....	110
		Acartia longiremis (Lilljeborg)..	60
Less numerous species (<50/100 m.^{3})		Less numerous species (<50/100 m.^{3})	
Oithona similis Claus.....	49	Tortanus discaudatus (Thompson and Scott)	20
Centropages hamatus (Lilljeborg).	40	Centropages hamatus (Lilljeborg)	18
Acartia longiremis (Lilljeborg)..	39	Calanoid sp. immature.....	8
Eurytemora herdmani Thompson and Scott....	15	Metridia lucens Boeck.....	8
Tortanus discaudatus (Thompson and Scott)..	14	Oithona spinirostris Claus.....	7
Acartia clausi Giesbrecht.....	12	Acartia clausi Giesbrecht.....	5
Euchaeta norvegica Boeck.....	2	Eurytemora herdmani Thompson and Scott....	4
Eurytemora sp.....	1	Calanus hyperboreus Kroyer.....	2
Oithona spinirostris Claus.....	1	Acartia sp. immature.....	1
Calanus hyperboreus Kroyer.....	([1])	Harpacticoid sp.....	1
Harpacticoid sp.....	([1])	Metridia longa (Lubbock).....	([1])
Calanoid sp. immature.....	([1])	Euchaeta norvegica Boeck.....	([1])
Cyclopoid sp.....	([1])	Anomalocera pattersoni Templeton.	([1])
Undinopsis similis Sars.....	([1])		

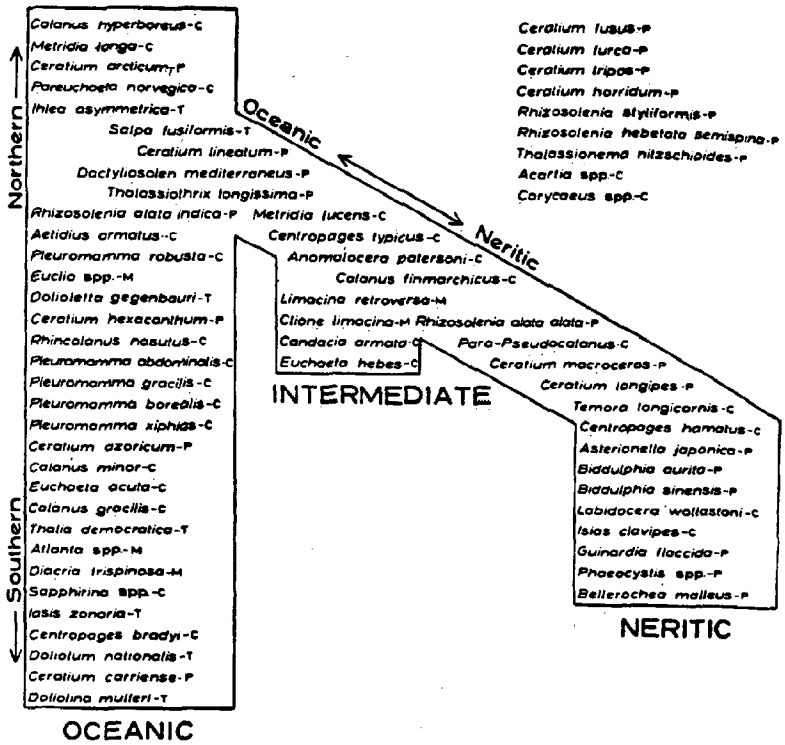
[1] Less than 1.

(Sherman, 1968)



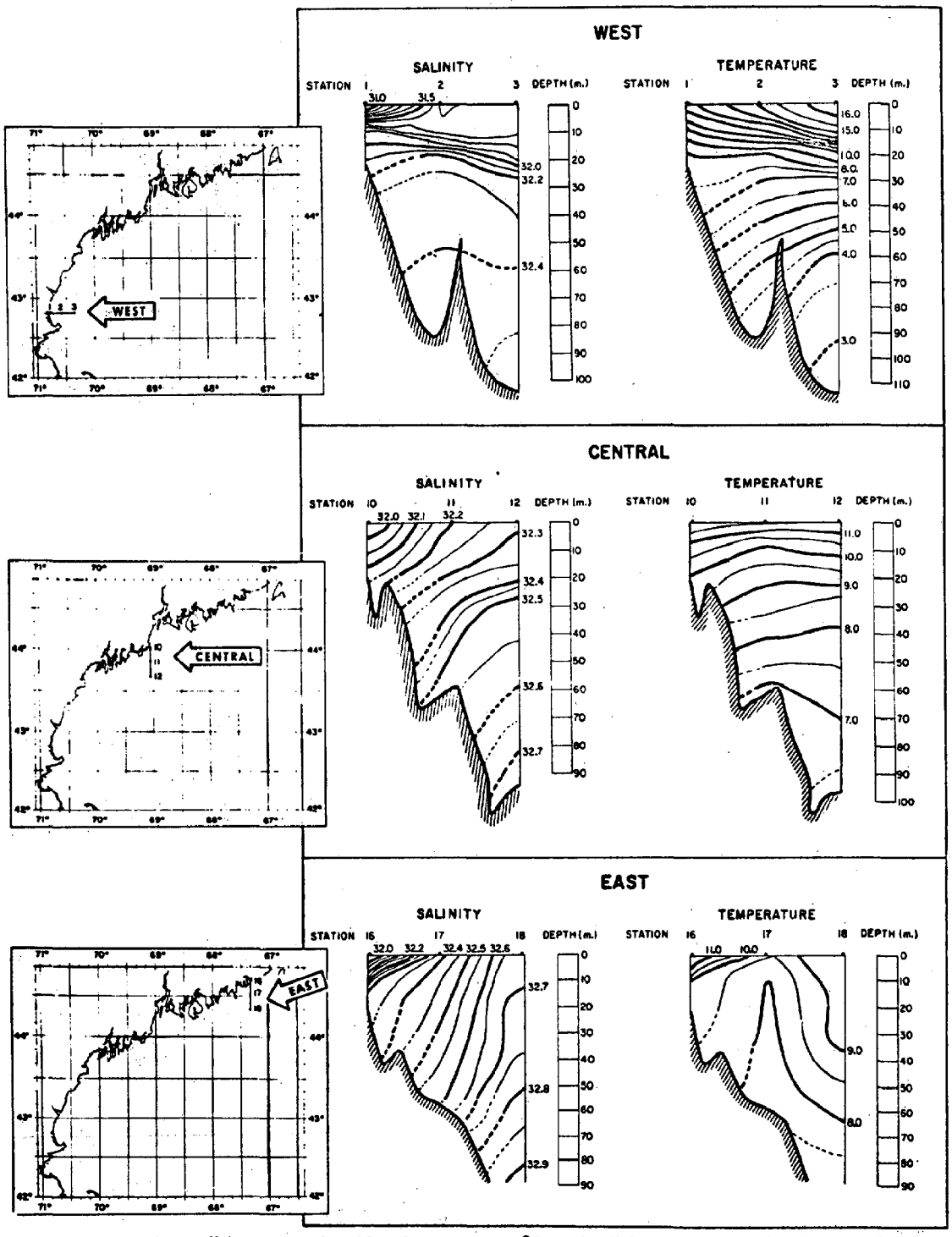
-Zooplankton sampling stations, Gulf of Maine coastal waters, 1965 and 1966.

Fig. 15a. Coastal plankton patterns in Maine (Sherman, 1968).



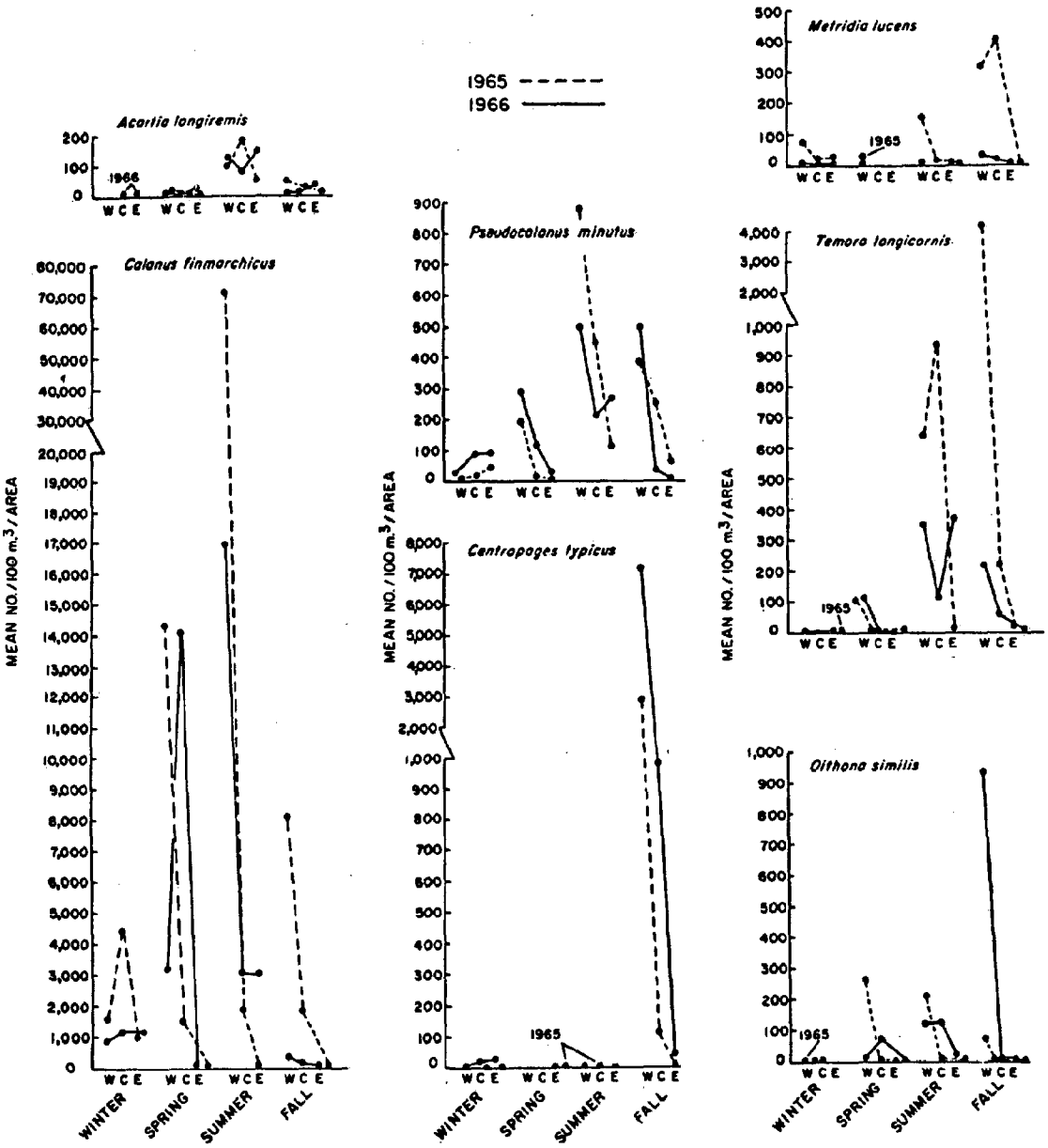
A biogeographic series for the northeastern Atlantic and the North Sea, derived from the Continuous Plankton Recorder Survey. The organisms are arranged so that the distribution of each species is similar to that of its neighbors in the series. P, phytoplankton; C, copepods; M, molluscs; T, tunicates (Colebrook *et al.*, 1961).

Fig. 15b. Comparison of principal plankton species in coastal zones(neritic) and oceanic zones (Glover, 1961).



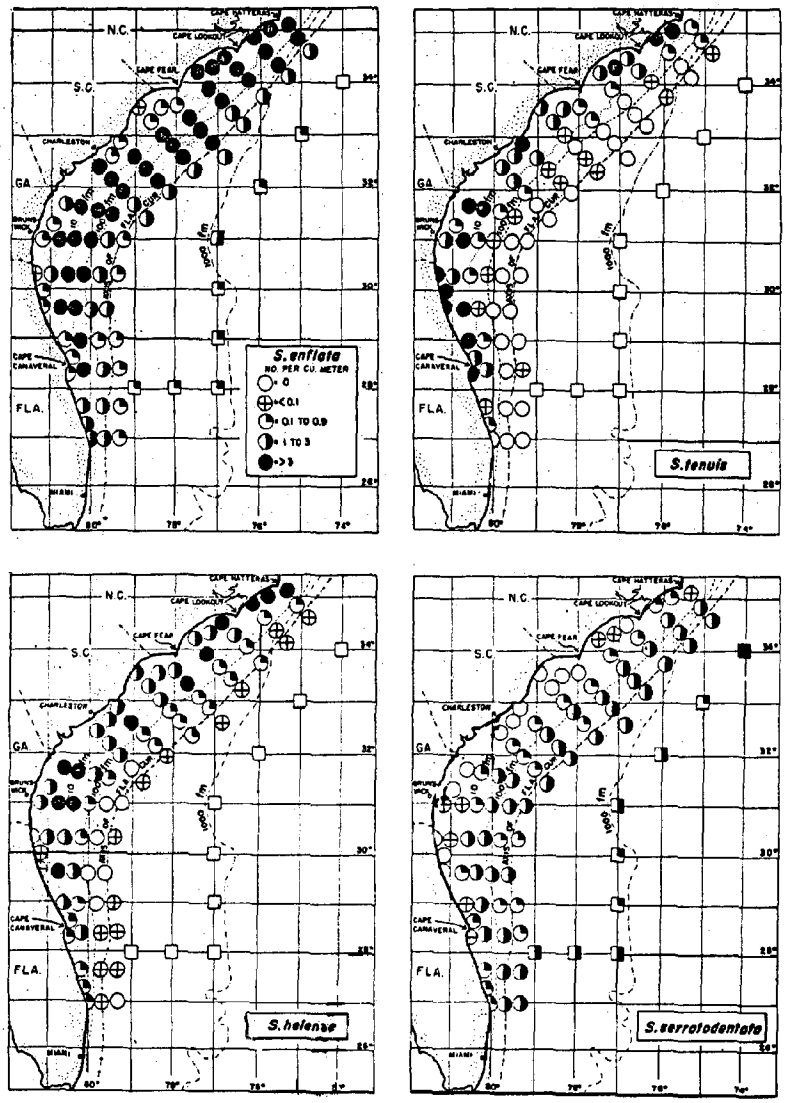
--Inshore-offshore vertical profiles of temperature (°C.) and salinity (p.p.t.), Gulf of Maine coastal waters, summer 1964. Insets at left show station locations.

Fig. 15c. Vertical sections of coastal hydrographic properties off Maine in summer (Sherman,1966b)



--Mean number of dominant copepod species per 100 m.^{3} of water in different seasons in each of the coastal Gulf of Maine areas, (W) western, (C) central, and (E) eastern, in 1965 and 1966.

Fig. 15d. Copepods of the coastal plankton zones of Maine (Sherman, 1968).



The distribution and abundance of *S. enflata, S. tenuis, S. helenae,* and *S. serratodentata*. The data have been averaged by station for the nine cruises.

Fig. 16. Arrowworms marking coastal plankton zones (Pierce and Wass, 1962).

Among the subsystems in the coastal plankton system are the scallop associations described by Wells, Wells, and Gray (1964) in Fig. 17.

DISCUSSION

The coastal plankton system holds its steady state patterns of chemistry and life because of the long-shore drift of its masses, because of gyrals that develop in concave parts of the coast, because of the effect of low salinity water in forming a circulating water mass, and because of the large storage in the bottom subsystems. Injections of waters from shore and open sea develop with weather systems. Stratification develops at times of heavy freshwater runoff. Sometimes estuarine plankton systems are displaced seaward during exceptional floods. The system has very high energies in its northern ranges. The presence of strong currents on the bottom allows development of microscale reef-like growths that can take advantage of the food filtering opportunities. The diagram in Fig. 19 by Riedl (1967) shows such an epifaunal cluster. See also Fig. 17.

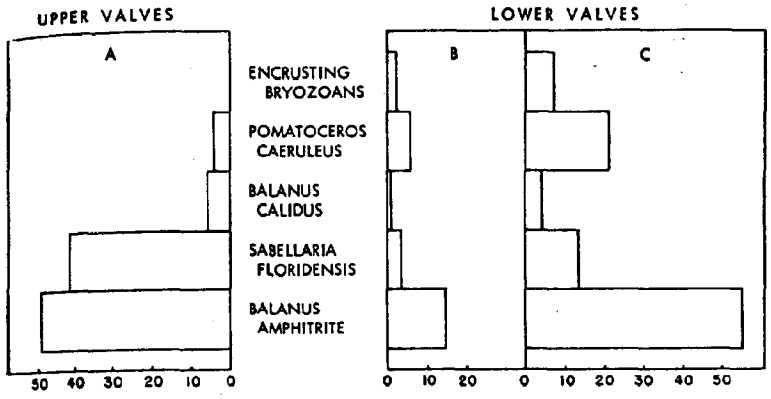
The effect of depth in dispersing and diminishing the amount of biological mass and activity was discovered in comparisons of large lakes and has often been observed in the coastal plankton system also. Decrease in bottom fauna with depth off Galveston, Texas is shown in Fig. 18.

The bottom subsystem is important in the coastal plankton ecosystems with bottom fishes, living on invertebrate food chains, a major yield of trawlers on fishing banks. The much studied ecosystem of the North Sea and English Channel in Europe with plankton food chains, herring, and bottom fishes provides perspective for understanding the U. S. coastal systems of similar depth. The year class phenomenon in the zooplankton eating herring fishes is characteristic, very large year classes dominating the fishery for several years. Apparently, the year class phenomenon provides storage and stabilizes the ecosystem where year to year plankton food changes are erratic. If a yearclass is overfished, a succession of poor year classes in developing larval fish can apparently eliminate the fishery. There may be a role of wastes in larval success. The sardine off California and diminishing Menhaden on the Atlantic Coast may be examples.

Summer Dinoflagellate Blooms and Toxic Clams

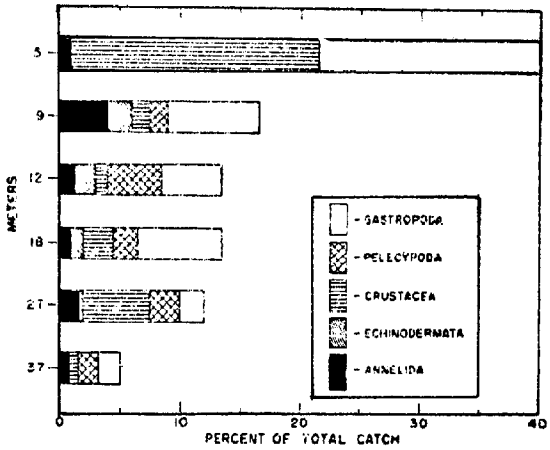
In the north temperate zone of both coasts of the United States, blooms of the dinoflagellate Gonyaulax develop in restricted waters in summer as shown in the example in Fig. 20. Mussels and clams, filter feeding in these waters absorb the poison and become toxic to man. Because of the threat of this poison, large potential harvests of shellfish in these zones are not taken. Apparently, in Indian times, these summer months were avoided for shellfish consumption. There is the interesting possibility that the clams and the dinoflagellates together constitute a protective symbiosis in which the toxin serves a regulatory role on consumption. For this to be a mutualism some action by the clams would be required in regenerating nutrients of quality encouraging the blooms of this type of phytoplankton. An understanding of this cycle of work mutualism might provide a basis for control and better utilization of the shellfish resource.

Schematic representation of a North Carolina calico scallop community. Included are *Balanus amphitrite, B. calidus, Pomatoceros caeruleus, Sabellaria floridensis,* and other common components of the faunal association.



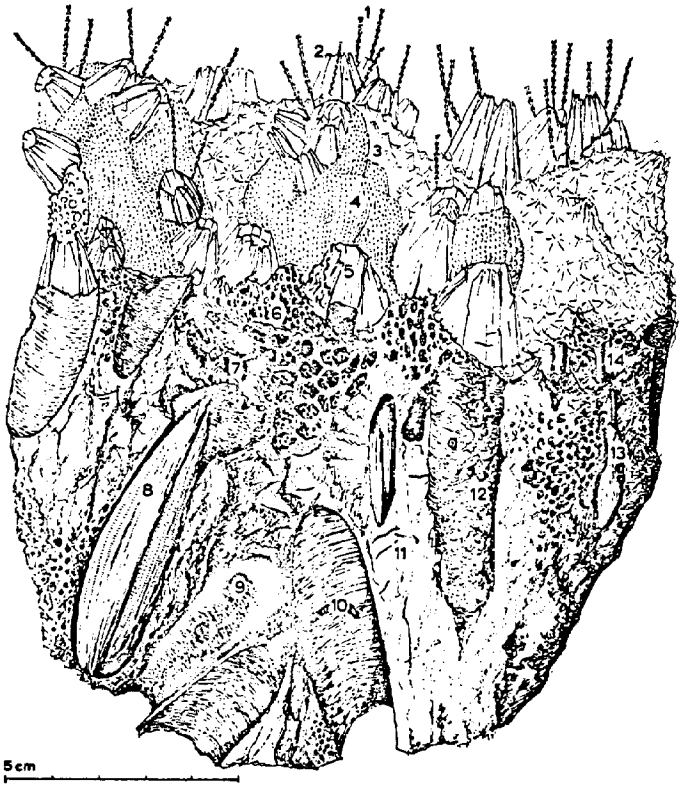
Comparison of total area occupied by dominant species on upper and lower valves. In A and B, coverage is indicated as a percentage of total area of the shell exterior. In C, coverage is indicated as a percentage of the total area occupied by fouling organisms.

Fig. 17. Ecological subsystem of the coastal waters of North Carolina (Wells, Wells, and Gray, 1964).



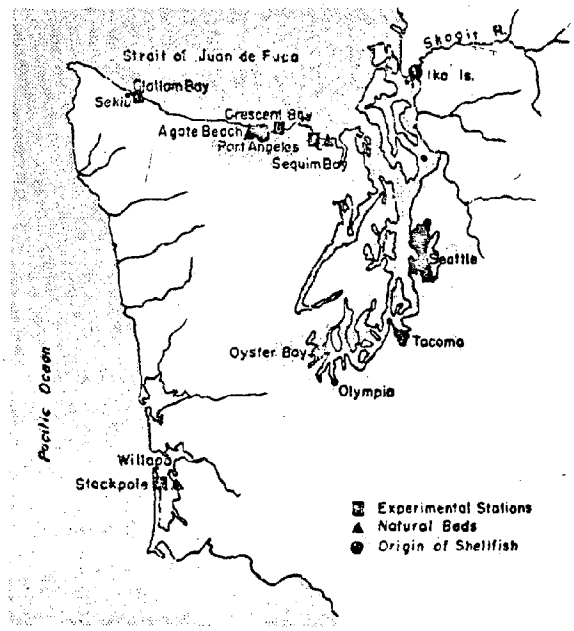
-Percentage occurrence by depth of bottom invertebrate groups collected off Galveston, Tex., January-February 1966.

Fig. 18. Decreasing biomass with depth (Moore,1967).

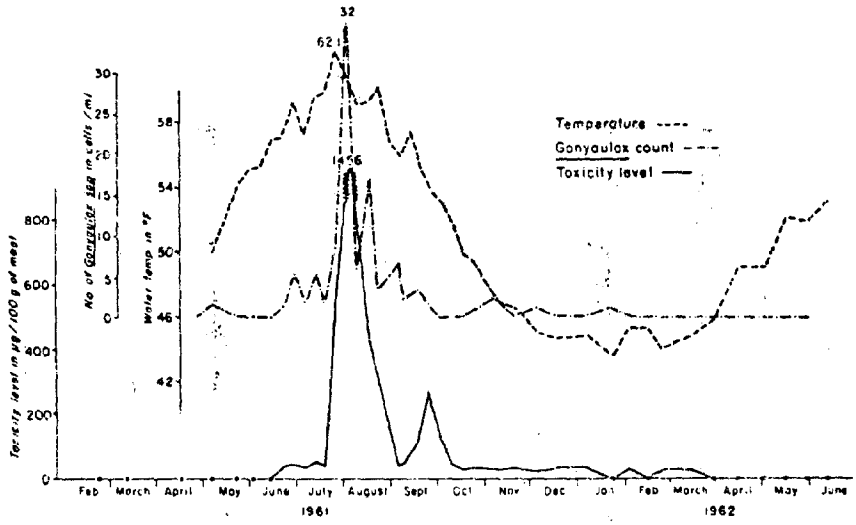


Detail eines Aufbaues mediterraner Höhlenbestände. Beziehung zwischen Endolithion und der darüberliegenden Krustenschichte Nr. IIa (vgl. Abb. 21). (Nach RIEDL 1966a)

Fig. 19. Epifaunal association in shelf waters (Riedl, 1967).



Site of experimental stations for paralytic shellfish toxicity study.



Toxicity levels in California mussel, numbers of *Gonyaulax*, and water temperatures, at the experimental float in Sequim Bay.

Fig. 20. Bloom of a poisonous dinoflagellate causing toxicity in shellfish (Sparks, Sribhibhadh, and Chew, 1963).

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